590.642
2
891
F.M.

TRANSACTIONS

OF

THE ZOOLOGICAL SOCIETY

OF LONDON.

VOLUME XVI.

LONDON:
PRINTED FOR THE SOCIETY:
SOLD AT THEIR HOUSE IN HANOVER-SQUARE;
AND BY MESSRS. LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

1903.

187349

SMITHSONIAN
LIBRARY

PRINTED BY TAYLOR AND FRANCIS,
RED LION COURT, FLEET STREET.

590.642

CONTENTS.

I. *On the Development of the Skeleton of the Tuatara*, Sphenodon punctatus; *with Remarks on the Egg, on the Hatching, and on the Hatched Young. By* G. B. Howes, *LL.D., F.R.S., and* H. H. Swinnerton, *B.Sc., Marshall Scholar R. Coll. Sci. Lond. (From the Huxley Research Laboratory.)* (Plates I.–VI.) . page 1

II. *Contribution towards a Knowledge of the Osteology of the Pigmy Whale* (Neobalæna marginata). *By* Frank E. Beddard, *M.A., F.R.S., Prosector and Vice-Secretary of the Society.* (Plates VII.–IX.) 87

III. *On the Breeding-habits of some West-African Fishes, with an Account of the External Features in Development of* Protopterus annectens, *and a Description of the Larva of* Polypterus lapradei. *By* J. S. Budgett, *M.A., F.Z.S., Trinity College, Cambridge.* (Plates X. & XI.) 115

IV. *Third Contribution to the Ichthyology of Lake Tanganyika.—Report on the Collection of Fishes made by Mr. J. E. S. Moore in Lakes Tanganyika and Kivu during his Second Expedition*, 1899–1900. *By* G. A. Boulenger, *F.R.S., F.Z.S.* (Plates XII.–XX.) 137

V. *On new or imperfectly-known Ostracoda, chiefly from a Collection in the Zoological Museum, Copenhagen. By* George Stewardson Brady, *M.D., LL.D., D.Sc., F.R.S., C.M.Z.S.* (Plates XXI.–XXV.) 179

VI. *On the Myology of the Tongue of Parrots, with a Classification of the Order, based upon the Structure of the Tongue. By* Geo. P. Mudge, *A.R.C.S. Lond., F.Z.S., Lecturer on Biology, London School of Medicine for Women; and Demonstrator of Biology, London Hospital Medical School.* (Plates XXVI.–XXIX.) 211

VII. *On* Okapia, *a new Genus of* Giraffidæ, *from Central Africa. By* E. Ray Lankester, *M.A., LL.D., F.R.S., F.Z.S., Director of the Natural History Departments of the British Museum, Correspondent of the Institute of France.* (Plates XXX.–XXXII.) 279

VIII. *On the Structure of the Larval* Polypterus. *By* J. S. Budgett, *M.A., F.Z.S.* (Plates XXXIII.–XXXV.) . . . . . page 315

IX. *Ecdysis, as Morphological Evidence of the Original Tetradactyle Feathering of the Bird's Fore-limb, based especially on the Perennial Moult in* Gymnorhina tibicen. *By* Edward Degen, *F.Z.S.* (Plates XXXVI.–XXXVIII.) . 347

List of the Papers contained in Vol. XVI. 419

Index of Species, &c. 421

TRANSACTIONS

OF

THE ZOOLOGICAL SOCIETY OF LONDON.

VOL. XVI.—PART 1.

LONDON:

PRINTED FOR THE SOCIETY,

SOLD AT THEIR HOUSE IN HANOVER-SQUARE;

AND BY MESSRS. LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

February 1901.

Price £1 4*s*. 0*d*.

Taylor and Francis, Printers,] [Red Lion Court, Fleet Street.

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

	To Fellows. £ s. d.	To the Public. £ s. d.
VOLUME I. (1833–1835, containing 59 Plates) . . Price	3 13 6	4 18 0*
VOLUME II. (1835–1841, containing 71 Plates) . . „	4 0 0	5 6 6*
VOLUME III. (1842–1849, containing 63 Plates) . . „	3 8 3	4 11 0*
VOLUME IV. (1851–1862, containing 77 Plates) . . „	6 2 0	8 2 6†
VOLUME V. (1862–1866, containing 67 Plates) . . „	5 4 3	6 19 0†
VOLUME VI. (1866–1869, containing 92 Plates) . . „	11 5 0	15 0 0†
VOLUME VII. (1869–1872, containing 73 Plates) . . „	10 4 0	13 12 0†
VOLUME VIII. (1872–1874, containing 82 Plates) . . „	9 8 3	12 11 0†
VOLUME IX. (1875–1877, containing 99 Plates) . . „	12 1 6	16 2 0†
VOLUME X. (1877–1879, containing 95 Plates) . . „	10 0 3	13 7 0†
GENERAL INDEX, Vols. I. to X. (1833–1879) . „	0 7 6	0 10 0
VOLUME XI. (1880–1885, containing 97 Plates) . . „	9 12 0	12 16 0
VOLUME XII. (1886–1890, containing 65 Plates) . . „	5 8 0	7 4 0

* No copies of these volumes remain in stock.

† Only complete copies of these volumes are left in stock.

Continued on page 3 of Wrapper.

TRANSACTIONS

OF

THE ZOOLOGICAL SOCIETY

OF LONDON.

I. *On the Development of the Skeleton of the Tuatara*, Sphenodon punctatus; *with Remarks on the Egg, on the Hatching, and on the Hatched Young. By* G. B. Howes, *LL.D., F.R.S., and* H. H. Swinnerton, *B.Sc., Marshall Scholar, R. Coll. Sci. Lond.* (*From the Huxley Research Laboratory.*)

Received May 21, 1900; read May 22, 1900.

[With Plates I.–VI. and 18 text-illustrations.]

Contents.

	Page
1. Introduction	1
2. Material	4
3. Methods and Reconstruction	7
4. Observations on the Egg, on Hatching, and on the Hatched Young	8
5. The Axial Skeleton	10
General, and as to Terminology	10
Vertebral Column	11
Ribs and Sternum	27
"Abdominal Ribs" (Gastralia)	34
The Skull and Visceral Arches	37
Cranio-facial Membrane-Bones	51
6. The Appendicular Skeleton	58
The Pectoral Girdle	58
The Pelvic Girdle	58
The Long Bones	60
The Carpus and Tarsus, with Phalanges	60
7. The Dentition	63
8. Summary and Conclusions	67
9. List of the more important Memoirs dealing with Sphenodon	71
10. Explanation of the Plates	75

1. Introduction.

All work in Reptilian Morphology during the last thirty years has increased the interest attaching to the creation in 1867 by Dr. Günther of the Order Rhyncho-

cephalia, which now, in its extended form, would appear to embrace a series of genera and species occupying a truly central position among the terrestrial vertebrates. Since the publication of Dr. Günther's memoir on Sphenodon, the discovery by Baur and others of its vomerine teeth, and by Spencer of its parietal-eye, have more especially increased our knowledge of this remarkable animal beyond that which is ordinary. One of its most distinctive characters is the forward prolongation of the pterygoids to meet the vomers with apposition in the middle line. The mere forward prolongation referred to is a feature already recognizable among the Batrachia and Stegocephalia; but special interest attaches to the median apposition, as there is little room for doubt that in that there lies the clue to the reduction and suppression of the parasphenoid in the ascending series of the Amniota. This important Rhynchocephalian character, long recognized in the Crocodilia and Dinosauria, has during recent years been discovered in the Ichthyosauria [1] and the Plesiosauria [2] by Lydekker and others, and probably in the Pterosauria by Newton [3], and it justifies the conclusion that the living Sphenodon may be the sole surviving representative of an early and widely ancestral amniote type. While the recent confirmation by Menzbier [4] and Pycraft [5] of Brandt's discovery in 1839 [6] that the Avian pterygoid may reach the vomer, with their further demonstration, that while this is a permanent feature of some Ratitæ and the Tinamous among the higher birds, this Rhynchocephalian character becomes lost during ontogeny under secondary segmentation and co-ossification of parts, as the progressively modified facial skeleton comes into closer relationship with the basis cranii, would seem to indicate an origin for the class Aves from some more primitive reptilian type than might otherwise have been supposed [7]—from something lower than the Dinosauria. Beyond this, Cope in 1870 [8], and Seeley in 1874 [9], have drawn attention to certain Chelonian resemblances in the Rhynchocephalia. In this they have been more recently followed by Boulenger, who regards [10]

[1] Lydekker, R.: Brit. Mus. Cat. Fossil Rept. & Amphib., Part 2, 1889, p. 5. *Cf.* also Baur, G.: Anat. Anz. Bd. x. 1895, p. 456; and (concerning the Rhynchocephalian affinity) Americ. Nat. vol. xxi. 1887, p. 337.

[2] Lydekker, R.: originally in *Pl. dolichodirus*, ibid. p. 257. *Cf.* also Andrews, C. W.: on *Peloneustes*, Ann. & Mag. Nat. Hist. (6) vol. xvi. 1895, p. 248, and on "The Structure of the Plesiosaurian Skull" in Journ. Geol. Soc. vol. lii. 1896, p. 246.

[3] Newton, E. T.: Phil. Trans. vol. 179 B. 1888, p. 503.

[4] Menzbier, M. v.: Bull. Soc. Imp. Nat. Moscou (n. s.), tome i. 1887, p. 492.

[5] Pycraft, W. P.: P. Z. S. 1898, pp. 973–974.

[6] Brandt, J.: Mém Acad. Sci. St. Pétersb. (vi.), Sci. Nat. tome iii. p. 81, & espec. pl. xvii. fig. 3 (*Rhyncops*).

[7] Provided the so-called "hemipterygoid" has the value claimed for it. It must not be forgotten that *Archæopteryx* appears to have had "abdominal ribs" (Dames, Palæontol. Abhandlg. Berlin, 1884, Bd. 2, p. 144), and that "intercentra" occur in most of the groups of non-Passeres among living birds (Beddard, P. Z. S. 1897, p. 465).

[8] Cope, E. D.: Proc. Americ. Assoc. vol. xix. 1870, p. 233.

[9] Seeley, H. G.: Journ. Linn. Soc., Zool. vol. xi. 1876. p. 183.

[10] Boulenger, G. A.: Brit. Mus. Cat. Crocodilia and Chelonia, 1889, p. 1.

" the affinities of the Rhynchocephalia to the Chelonians as at least as great as to the Lacertilia;" while almost the first observation made in the development of the Tuatara was that by Dendy (98, and 99[b]. p. 66) of the post-amniotic canal, which, though probably of wide occurrence, was originally discovered[1] and is at present known elsewhere only in the Chelonia, and of the horny "shell-breaker," which, being of the Chelonian type[2], places Sphenodon in sharp contrast to the Lacertilia, which, so far as is known, develop a calcified "egg-tooth."[3]

Far reaching as is thus the interest arising from a comparison of the recent Sphenodon with representative members of the living orders of Reptiles, that with certain extinct orders and suborders other than those already alluded to is even more suggestive. The discovery by Credner in the Permian deposits of Saxony of the assemblage of vertebrate forms he has so aptly termed[4] the "Eotetrapoda," and more particularly the genus he has less aptly named Palæohatteria, has materially lessened the structural gap between the Reptilia and the Stegocephalia; while the description by Lortet, eight years ago, of Rhynchocephalian remains[5] from the Upper Jurassic of the Rhone Basin which reveal new cranial characters, with that of Crocodilian resemblances in *Champsosaurus*[6], which, like *Acrosaurus*[7], is believed to have been aquatic in habit, shows the Rhynchocephalian Order, now all but extinct, to have been in the past extensive and subject to considerable modification. It is now generally conceded that the Anomodontia (Theriodontia and Pariasauria) in some respects stand on an even lower structural level than the Rhynchocephalia; and, this being so, the recognition among these of Rhynchocephalian characters—originally by Seeley in *Procolophon* in 1878[8]—only the more fully justifies the belief in the primitive nature of the Rhynchocephalian

[1] Mitsukuri, K.: Journ. Sci. Coll. Tokyo, vol. iv. 91, p. 10. *Cf.* also Dendy, 99[c]. pp. 251 & 255.

[2] *Cf.* Dendy, A., 99[c]. pp. 56 & 59, and Parker, W. K., 'Challenger' Reports, Zool. vol. i. pl. 3. fig. 1.

[3] *Cf.* Leydig, F.: 'Die in Deutschl. lebend. Arten d. Saurier,' Tübingen, 1872, p. 110; and Boulenger, G. A.: on the Ophidian *Aipysurus annulatus*, in Willey's 'Zoolog. Results,' Cambridge, 1899, p. 57.

[4] Credner, H.: Allgem.-Verhandl. Naturwiss. Abhandlg. Berlin, Hft. xv. 1891, pp. 1–52.

[5] Lortet, L.: Archv. Mus. Hist. Nat. Lyon, Bd. v. 1892, pp. 139. It is interesting to note that *Sauranodon* possessed procœlous vertebræ.

[6] Dollo, L.: Bull. Soc. Belge d. Géol., tome v. 1891, p. 151.

[7] Andreæ, A.: Ber. Senckenbg. Naturf. Gesellsch. 1893, p. 21.

[8] Seeley, H. G.: Quart. Journ. Geol. Soc. vol. xxxiv. 1878, p. 803. The pterygo-vomerine relationship is now known to be Rhynchocephalian among Anomodonts in Procolophon and Galesaurus (A. S. Woodward, 'Outlines of Vertebr. Palæont.,' Camb. 1898, pp. 148 & 152), and it is probably so in Pariasaurus also (*cf.* Seeley, Phil. Trans. vol. 183 B. 1892, p. 317). The description of a post-palatine fossa, which in all probability received a median tonsil ("bursa pharyngea") like that observed by Killian (Morph. Jahrb. Bd. xiv. 1888, pp. 659–690) for living reptiles, as the posterior nares, and of the true posterior nares (p. 317) as "anterior comma-shaped palatal vacuities," is erroneous. The study of the palatal region of this animal needs re-investigation.

Order, and of Sphenodon, its living representative. Since Sphenodon thus occupies the afore-mentioned primitive position among living reptiles—not to say among the Sauropsida as a whole—and since our classificatory systems of the Vertebrata, to be of avail, must be primarily based upon facts concerning parts capable of fossilization, the special interest attaching to the study of the development of the Sphenodon skeleton becomes sufficiently evident. And, as involving the Order Rhynchocephalia, the fact that in one of the most recent, and that which we have found the most rational and serviceable of classifications thereof[1], a distinction has become possible between a higher and a lower sub-order, in itself raises the interesting question whether in the development of Sphenodon, a member of the higher sub-order, there may not be passed through phases characteristic of the lower, to-day unrepresented.

During the thirty years afore-named no available opportunity has been lost by workers of all nationalities to study the habits and anatomy of Sphenodon, and a list of the resulting papers is appended to this Memoir (*infra*, p. 71). Most organs and systems have received attention. The most exhaustive contribution is that of the Japanese Osawa, which is a laborious anatomical treatise extending over 438 pp. of the Archiv für Mikroskopische Anatomie (*cf.* list, Osawa, 96–98); and, while grateful to him for this, it is with much astonishment that we have to record his final conclusion (98 [b]. p. 352, and 98 [c]) that Sphenodon is an Agamid—a reversion to the view of Gray (1831), adopted and afterwards forsaken by Cope[2], revived by Peters (70), and rejected by Günther (69. p. 624)[3].

2. Material.

In 1894, when Professor Dendy was appointed to the Chair of Biology in the Canterbury College of the New Zealand University, one of us, in regular correspondence with him, sought to impress upon him the desirability of doing all in his power to secure without delay material for the study of the development of Sphenodon, not knowing at the time that our mutual friend, Prof. Baldwin Spencer, F.R.S., of Melbourne, had also approached him on the subject. With what enthusiasm and at what personal cost he responded to the desire, his published memoirs (Dendy, 98, 99[a], 99[b]) amply testify. On hearing of his success in the field, no time was lost

[1] Boulenger, G. A.: Ann. & Mag. Nat. Hist. (6) vol. xi. 1893, p. 204.

[2] Cope, E. D.: *cf.* Proc. Acad. N. S. Philad. 1864, p. 227, and Proc. Americ. Assoc. vol. xix. 1870, p. 233.

[3] It has always been to me inexplicable why Huxley should have refused to admit the validity of the Order Rhynchocephalia. Well do I remember how, in conversation, he once remarked to me that "Sphenodon is a lizard and only a lizard!" but, this notwithstanding, his final printed statement and proposal to create, for the reception of *Hyperodapedon*, *Rhynchosaurus*, and *Sphenodon*, the group of the "Sphenodontina" (Quart. Journ. Geol. Soc. vol. xliii. 1891, p. 691) would seem indicative of a compromise suggestive of an approaching conviction.—G. B. H.

in drawing his attention to certain of the more interesting problems (duly set forth in the pages of this Memoir) presented more especially by the skeleton and teeth of the adult animal. In reply, he expressed the hope that one of us would undertake this portion of the work, and offered, with a generosity and friendly appreciation for which we tender him our heartiest thanks, to give all the necessary material he could command if we would acquiesce. There accordingly reached us in the autumn of 1898 a large series of specimens, treated, for the younger stages with corrosive sublimate and alcohol, for the older with alcohol alone. From these, after preliminary examination, the undermentioned were selected, as embracing the period of skeleto-genesis; and, concerning those which remain, Prof. Dendy has very generously acquiesced to the proposal that Dr. Elliot Smith and Mr. E. J. Bles, of Cambridge, should work out respectively the development of the brain and urinogenital organs.

List of Young Specimens Investigated (15 *in all*).

Stage.	No.	Date of removal from Egg.
P	87.	Jan. 25, 1898.
P*	39 *a*.	Unknown.
Q*†	52 *a*.	Jan. 30, 1899.
Q	1 *a*.	End of Jan. 1897.
R	142.	March 8, 1898.
R	154.	April 5, 1898.
R	159.	May 12, 1898.
R	162.	June 24, 1898.
R–S†	I.	
S†	II.	
S†	IV.	
S*	1 *a*.	Hatched Dec. 8–9, 1898.
S*	19 *a*.	,, Dec. 27, 1898.
S	138.	No details.
T†	III.	

The following are the details concerning the individuals incubated and afterwards reared in our own Laboratory.

Stage.	Length in cms.	Remarks.
R–S$^{I.}$	6·3	Died in egg, 13.11.98.
S$^{II.}$	7·5	Hatched prematurely with excessive yolk, 22.11.98.
T$^{III.}$	15	Hatched 14.1, died 1.5.99.
S$^{IV.}$	...	Found decomposed in egg, 14.1.99.
T$^{V.}$	15	Hatched 19.1, died 18.5.99.
T$^{VI.}$	17	,, 24.1, died 18.5.99.

In the foregoing list the stages and numbers are those of Dendy's series, described in the Quart. Journ. Microsc. Sci. vol. xlii. p. 10. Those marked * were found requisite as our investigation advanced, and were very kindly supplied by him at our request, and those marked † were incubated in our own Laboratory from unhatched eggs. The latter, six in number, packed close in moist sand in a 1-lb. canister with a perforated lid, were brought over by Mrs. Dendy and kept during the voyage from New Zealand in her cabin. One only decomposed, and of the five which remained, three ran the full developmental period, the enclosed young making good their own escape. These lived from three to four months, and for their reception we have added to Dendy's series a Stage T. At this stage the coloration is the same as at S, but as an advance upon that there is a complete absence of all traces of the yolk-sac and shell-breaker, and the appearance in the thoraco-lumbar region of the all characteristic median dorsal languets (spines, *auct.*), such as are already present at Stage S in the so-called "nuchal" and the caudal tracts. These appendages, whose existence is expressed in the native name Tuatara [1], are liable to no slight individual variation. Three tracts are present in the adult, viz. "nuchal," thoraco-lumbar ("dorsal"), and caudal, as recognized by Boulenger in his, the latest, diagnosis (89. p. 2), with consequent scapular and sacral intervals. Buller (76. p. 324) and Newman (77. p. 230) have called attention to the existence in the region of the cervical space of a conspicuous pigment-patch; and, concerning the numerical variation of the "spines" in the adult, they give for the "nuchal" series 10–14, for the thoraco-lumbar 15–20. From examination of eleven specimens present in our own collection and that of the British Museum of Natural History, we find the extremes range from 6 to 14 for the "nuchal" and 15 to 24 for the thoraco-lumbar series. In two specimens of our Stage T they number 10 and 18 respectively.

With a view to ascertaining the limits of individual variation, and thereby rendering the present memoir as complete as possible anatomically, we have examined all the dried skeletons within our reach—viz., the complete skeletons of nine adults, fragments of some six to eight others, and the complete skeleton of a half-grown individual in the possession of the Royal College of Science, Dublin. For the privilege of examining all but two, which are at South Kensington, we are indebted to Prof. A. C. Haddon, F.R.S., to Prof. C. Stewart, F.R.S., of the Royal College of Surgeons Museum, to Dr. R. F. Scharff, Keeper of the Natural History Department of the Science and Art Museum at Dublin, and to our friends in the British Museum of Natural History.

Beyond this, we have had recourse where necessary to dissection of six spirit-specimens in the Teaching Collection of the Royal College of Science, two of which were presented by Prof. Dendy in the spring of 1899.

[1] *Cf.* Newman (Taylor *cit.*), 77, p. 222.

3. Methods and Reconstruction.

Methods.—Dissection was resorted to only in the later stages, and wherever the elements under consideration were fully formed. Throughout the earlier stages, and in the later where necessary, microscopic sections were relied upon; and further, as for example at Stage S and in dealing with the carpus and tarsus, dissection was duly checked by section, as a means of ensuring accuracy of detail.

The microscopic sections were in all cases mounted serially, the plane of section being determined by the object in view (as set forth in the accompanying description of the Plates). After preliminary experiment with the Green Lizard (*Lacerta viridis*), it was found that differentiation of the skeletogenous tissues could best be obtained by staining in bulk with Ehrlich's hæmatoxylin, and afterwards on the slide with Grübler's orange G. For this suggestion and much subsequent aid we are indebted to Mr. M. F. Woodward, Demonstrator of Zoology, Royal College of Science, London, than whom no better manipulator or master of micro-chemical technique exists; and we found, as our work proceeded, that much time is to be saved by dissolving the orange in 70 p. c. alcohol, with the addition of a few drops of glacial acetic acid, thus eliminating the tedium arising out of the use of a mere aqueous solution. The results of this method are exceedingly satisfactory, cartilage being as a rule differentiated blue, bone in all its forms deep yellow, while the other tissues behave each in its own way.

Reconstruction.—Since the time has now arrived at which mere dissection is insufficient for the study of the facts of skeletogenesis, recourse was had to the so-called Bornean method of reconstruction from microscopic sections[1]. We were under the necessity of working with thin plates, and found that if made of the Bornean mixture of beeswax and turpentine there was difficulty in preparation and liability to snap. By substituting vaseline for turpentine, we entirely overcame all this, and we can confidently recommend our mixture as reliable.

The figures which constitute Pl. III. and figs. 7 and 10 of Pl. VI. are all from models prepared from plates thus made. For the most part the sections of the animal were cut to a uniform thickness of 10 μ, and each plate made to that of 1 millim. Tracings were then drawn upon the plates, by means of the camera lucida, of sections at regular intervals, determined by the degree of magnification (every fourth section for a magnification of 25, every third for that of 33, and so on). In cutting out the tracings, trabeculæ were left where necessary for holding the parts together during reconstruction, and afterwards cut away. For the process of cutting, the best results were obtained by the use of a needle, the plates being laid upon glass

[1] Earlier achievement in the same direction must not be overlooked. In England it stands memorably associated with the Huxleyean traditions: *cf.* E. T. Newton, "On a New Method of Preparing a Dissected Model of an Insect's Brain from Microscopic Sections," Journ. Quekett Microscop. Club (I.), vol. v. 1878, p. 150, and Qu. Journ. Micr. Sci. (n. s.) vol. xix. p. 340.

The tracings, as cut out, were laid flat in superposition, adhesion being effected by carefully running a heated wire along their edges. The use of colour was deemed desirable, but a possibility of error seemed likely to arise were the models coloured after completion. This, however, was obviated by colouring the tracings before they were cut out; and a perfectly reliable result was obtained by the use of ordinary oil-paint dissolved in xylol, to secure rapidity in drying. In plates thus treated, the melting together of their edges ensured the diffusion of the colour necessary to produce the final realistic result.

4. Observations on the Egg, on Hatching, and on the Hatched Young.

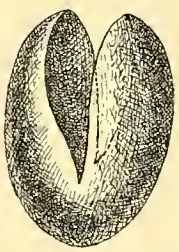
During the period of Prof. Dendy's activity, both as collector and investigator, which led to the publication of his two pioneer memoirs on the Development of Sphenodon (Dendy, 98[b], 98[c]), there arrived in New Zealand two German naturalists—one Dr. H. Schauinsland, of the Bremen Museum, the other Prof. G. Thilenius, of Strasburg; one, if not both, of them sent out under the auspices of the Berlin Academy. Each has since published preliminary reports upon his investigations (*cf.* List, p. 74), without, however, in any way alluding to Dendy's work; and this is the more regrettable, since in matters of small detail their statements both differ from and supplement his—while it is the more unaccountable, since one of them was permitted by the New Zealand Government to explore the same island as Dendy, with the aid of the very collector he had employed. Since neither of them has written upon the skeleton, we omit further reference to their work, except so far as it concerns the newly-hatched young. Dendy, in defining his Stage S, inclined (99[a]. p. 59) to the belief that the yolk is still pendant at hatching, and was unable to decide definitely upon his surmise (pp. 79–80) that the olfactory cellular-plugs which he discovered are at that period "removed." Schauinsland, on the contrary, both figures the yolk and describes the nasal plug as absorbed shortly before hatching (98[c]. p. 312), and there can be no doubt he is correct. It is but just, however, to Prof. Dendy to state that in a letter to one of us, antedating the publication of Schauinsland's notes, he had corrected his former statements (*cf.* letter to 'Nature,' vol. lix. p. 340), having discovered that the embryos which had led him to believe that both yolk and plug might be present on leaving the egg had been prematurely hatched.

Concerning the newly-hatched young, he further points out that the pineal eye is "plainly indicated by an irregular scale, surrounded by eight or nine others, radially arranged, and all much larger than the surrounding granules," an observation which we can confirm. And to this we would add that the supra-pineal area of the skin of the head is at hatching transparent and pigmentless, and that it remained in that condition throughout the four months our young ones were alive.

Before passing to the main subject of this Memoir, we desire to record some observations pertinent to those communicated by us, in conjunction with Dr. Dendy,

in the above-mentioned letter to 'Nature.' Firstly as to the rupture of the egg-shell, to the symmetrical "clean cleft" character of which we drew attention. The following is a drawing of the shell of one of the eggs therein referred to which ran the full time; and in correspondence with Prof. Dendy concerning it and our suggestion that it seemed to indicate that the shell-breaker may be an actual cutting-instrument, he has authorized us to state his own view, since formed, on opening an egg at Stage S, nearly ready to hatch. He observed that the moment a small puncture is made in the shell, that "splits of itself, very suddenly and with almost explosive violence, reminding one of the bursting of a seed-vessel;" and he remarks that it has been suggested to him that the splitting may have been assisted by

Fig. 1.



Ruptured egg-shell of *Sphenodon* after the escape of the enclosed young.
Full time. Nat. size.

absorption of moisture from without, by the allantoic fluid[1]. He reverts to the analogy of the well-known "Prince Rupert's drops," and concludes that "the function of the very sharp shell-breaker is probably to make the small incision;" and that when that is done, the egg, being in a condition of high tension, simply bursts open. And he is the more inclined to this view from having noted that the shell of an egg contained in sand which had been "somewhat excessively moistened" prematurely burst, and revealed within its interior a dead embryo in an insufficiently advanced stage of development.

In the afore-mentioned letter to 'Nature' we recorded certain details concerning the treatment up to the time of hatching of the eggs brought us by Mrs. Dendy. The three young Sphenodons which from these we successfully hatched out were kept in confinement in the incubator (Hearson's, size A I.), at the temperature at which they were hatched—viz. 25° Centigr. They were fed upon mealworms, small earthworms, cockroaches, and flies, as best obtainable. For these the individual taste was observed to vary somewhat. One little creature exhibited a decided preference for mealworms, and a "tug-of-war" for the possession of an earthworm or cockroach was a not unfrequent occurrence.

[1] *Cf.* also Dendy, 99[c]. p. 251.

The bottom of the vivarium was covered with coarse sand to a depth of about one inch, and in one corner a water-bath was sunk; while a piece of corky-bark was introduced, which presented to the little captives a vaulted retreat. While to the latter they would readily retire, they exhibited a decided preference for the darker recesses of the chamber. Their movements during the day-time were very active, the passing of a finger-tip, the point of a pencil, or a piece of india-rubber tubing over the glass front of their dwelling, being sufficient to entice them forward. The tendency to burrow evinced itself during the second month—the actual date of the first effort being March 9th in one case observed. They exhibited a fondness for reclining in the water, in which they would lie at full length, the top of the head being usually kept above the surface. It was noticed that when, on leaving the water, the whole body was wet, an area surrounding the pineal eye always remained dry; and, concerning the use of the "bath," it was observed that if an earthworm seized by the Lizard happened to be beset by sandy particles, recourse was had to the water and a "washing" of it before it was devoured. The prey was never swallowed as soon as seized, but always at first held between the jaws and more or less masticated.

The first ecdysis in the case of the largest specimen (T$^{VI.}$ p. 5) was observed to take place about March 9th,—*i. e.* about 7 weeks after hatching.

Under the conditions above-described our little Sphenodons thrived and grew fat; *i. e.* they increased in length during the four months we kept them alive from 8 cm. to 15–17 cm. The near occurrence and manner of their decease, however (all three having died in the "bath" within a period of 17 days), points to a common cause of death. We suspect that this may have arisen from our having unconsciously continued to liberally feed them into the period normal to hibernation (April to middle of August[1]); but, on the other hand, it may have been the mere result of over-feeding on our part (if indeed that may not have been in turn aided by the attentions of night-watchers and others who were "interested"). Whichever be the case, the salient feature of the dead animals was a superabundance of fat; and we found *post mortem* that this was evident externally in life, had we but known it, in the great enlargement and tenseness—due to its accumulation—of the dorsal languets and certain irregular folds of the skin originally described by Gray[2]; *i. e.* that undue distension of these may be an index of over-feeding—an observation to be borne in mind by those who may yet be so fortunate as to rear this species in captivity.

5. The Axial Skeleton.

General and as to Terminology.—The adult skeleton of Sphenodon has been so fully described in its modern aspects by Siebenrock (93) and Osawa (98 [c]) that recapitulation of its general features is here unnecessary. Before, however, we proceed to details

[1] *Cf.* Schauinsland, 98, p. 702 (for Stephen's Island).

[2] *Cf.* Gray, 42, p. 72.

and the study of its development, we desire to deal briefly with certain facts and matters of terminology which are necessary to render clear our method of procedure. Admitting for the vertebral column of all terrestrial vertebrata a primary classification of the parts in relation to the sacrum, the time-honoured classification of the præ-sacral portion of that of the Amniota into cervical, so-called "dorsal" or thoracic, and lumbar regions, is now wholly insufficient for purposes of accurate description and comparison. The term "dorsal," being one of orientation, is misapplied. "Thoracic," although applicable to the middle region in the mammal—as embodying the region enclosed by elongated rotatable ribs and bounded posteriorly by the diaphragm—cannot with precision be applied to that of the lower Amniota, inasmuch as it presupposes the existence of a post-cardiac septum (diaphragm). The so-called "diaphragm" of birds (Huxley's "oblique septum") is præ-cardiac, and the subdivision of their cœlom into pulmonary and cardio-abdominal compartments is in marked contrast to that of mammals, which is pulmo-cardiac (or thoracic) and post-cardiac (or abdominal). Further, when it is remembered that within the reptilian series various modes of cœlomic subdivision occur, and that free ribs in both birds and reptiles may extend beyond the limits of the pulmo-cardiac region, the application of the term "thoracic" to the whole of that portion of the body which bears them is apt to lead to confusion. And when, in addition, there are considered the presence of free ribs in the lumbar region of at least the young of some mammals [1], the great variation of the ribs both in the lumbar and cervical regions of the Amniota generally, and especially that of the sternum in all its relationships, simplicity and greater uniformity in our ideas are to be ensured by enumerating the several segments of their præ-sacral vertebral skeleton by reference to the sternum—and we accordingly propose to substitute the terms *præsternal*, *sternal*, and *poststernal*, for the more familiar but arbitrary "cervical," "thoracic," and "lumbar," delimitating the regions by reference to the one organ which renders a series of terms necessary [2].

Vertebral Column.—Concerning the adult vertebral column as a whole, we have not met with any numerical variation of its parts beyond that involving the relationships of the sternum duly considered in the sequel. For the caudal region the maximum number of vertebræ observed by us was 34 (two less than that originally recorded by Günther [67. p. 605]), and for the præcaudal we found it always 27, viz., præsternal 8, sternal 3–4, poststernal 13–14, sacral 2, with one exception for the præsternal series. To an exceptional condition of the sacrum in another individual we shall return.

During the past fifteen to sixteen years the study of the detailed constitution and early development of the vertebral column has received an altogether exceptional amount of

[1] *Ex.* Homo, juv.: Rosenberg, Morph. Jahrb. Bd. i. p. 111.

[2] On the other hand, it has been pointed out by one of us ('Nature,' vol. lvii. p. 577) that in the Batrachia, in the absence of a costal sternum, delimitation becomes possible only in relation to the sacrum, whereupon the præsacral vertebræ are best dealt with collectively. The same principle applies to those Amniota in which the sternum has been lost; while in the absence of a sacrum, as in the Ophidia, the course is obvious.

attention, mainly as the result of palæontological discovery by Cope [1], Gaudry [2], and Fritsch [3]; leading to the recognition of the so-called rhachitomous, embolomerous, and other similar conditions, which have received at the hands of subsequent investigators correspondingly appropriate names. Both on the embryological and the palæontological sides, a considerable amount of evidence has been brought forward for the belief that some such complex type of vertebra as these, *i. e.* one in which each vertebral segment was made up of a series of paired elements, was the ancestral one, and that the various types of vertebral structures characteristic of the living groups may have resulted from diverse modification (inequality of growth and suppression) of these. And, in the attempt to substantiate this belief, Männer, in the latest paper [4] on the subject, has sought to show that from the first period of its differentiation in cellular tissue, the individual "sclerotome" of the Lacertilian is a compound structure. Goette, basing his arguments, like Männer, mainly upon the study of the Reptilian backbone, has concluded [5] that the vertebræ of the living "digitata" have arisen from the embolomerous type, and he regards the rhachitomous type as "neither primitive nor independent, but transitional." If, however, the relationships of these are really direct, we would rather transpose the order, since we regard the greater extension of the skeletogenous tissues, and consequent deeper constriction of the notochord, occurring in the embolomerous type as indicative of advance upon the rhachitomous, as already pointed out by Gadow [6]. He, working on this basis, has simplified our conceptions of the fundamental constitution of the diverse forms of vertebral structure represented among the living vertebrata, beyond his predecessors, by the introduction of a systematic terminology based on the supposition that all surviving forms of vertebræ are constituted more or less of two pairs of dorsal and two of ventral elements symmetrically disposed, and that [7] "the solution of the composition of the vertebral column is given by the metameric repetition" of these, "the origin of which can be traced in fishes." His terms "basi-" and "inter-" "dorsalia," "basi-" and "inter-" "ventralia," are most welcome; and the arguments and conclusions drawn by him certainly furnish a possible explanation of some of the great anomalies arising out of the mere study of the adult vertebral column among living forms—as, for example, the intervertebral disposition and independence of the "chevron bones" of the Amniota, and the vertebral disposition and confluence with the vertebral bodies of the "hæmal arches" of the Urodela.

[1] Cope, E. D.: Americ. Nat. 1878, p. 327; Proc. Americ. Philos. Soc. vol. xvii. 1878, pp. 510–526; Trans. Americ. Philos. Soc. vol. xvi. 1886, p. 243.

[2] Gaudry, A.: Enchainements d. Monde anim. Foss. Prim., tom. i. (Paris, 1883), p. 263.

[3] Fritsch, A.: Fauna d. Gaskohle d. Permform. Böhmens, Bd. ii. 1889, pp. 14 & 24. *Cf.* also Baur, G.: Biol. Centralbl. Bd. vi. 1886, pp. 332 & 353.

[4] Männer, H.: Zeitschr. wiss. Zool. Bd. lxvi. 1899, p. 43.

[5] Goette, A.: Zeitschr. wiss. Zool. Bd. lxii. 1897, p. 390.

[6] Gadow, H.: Phil. Trans. vol. 187 B. 1896, p. 1.

[7] *Op. cit.* p. 50.

Certain it is that this subject, as it now stands, forms one of the most fascinating chapters in the vertebrate morphology of our time. Our own researches begin at the period of differentiation of actual skeletogenous tissue, and while, concerning the supposed original complexity and general uniformity in origin of the parts of the vertebral body, we retain an open mind, we question if, in matters of detail to be referred to in the sequel, theories, in their growth, have not been at times unconsciously read into the supposed record of facts.

First differentiation of the Skeletogenous Tissue.—The earliest stage which we have investigated is Dendy's P, and a median longitudinal section through any portion of the skeletal axis at this stage reveals the presence of a central notochord, ensheathed in a thin structureless and deeply staining cuticle or *chordal sheath* (elastica externa of Gadow [*nc.s.*, Pl. I. fig. 2]). This is seen to be in turn invested by a continuous *skeletogenous sheath*, composed of a thickly disposed mass of small cells, containing relatively large nuclei. There are some 9–10 rows of these, and their close compression gives to the tissue, when examined under a low magnifying power, the appearance of being feebly longitudinally striate. The notochord itself consists at this stage of comparatively small vacuolated cells, arranged in an irregular manner, and differentiated peripherally into the usual *chordal epithelium* (*nc.e.*). Central or other differentiation there is none.

Comparing with the foregoing a lateral longitudinal section, the superficial cell-rows of the skeletogenous layer are seen to be more closely approximated than the rest, and in addition there are (fig. 1) differentiated within the area of this more closely aggregated stratum a series of metamerically recurrent masses (*i.p.*) of cells, generally more rounded than the rest. They are the developing intercentra; wherefore it follows that in order of differentiation these are the first formed skeletal elements.

When the corresponding parts are viewed in transverse section, the skeletogenous layer is seen to completely encircle the notochord, constituting a *skeletogenous sheath*, the aggregation afore-named being apparent (*i.p.*) as a couple of symmetrical tracts which are ventro-lateral, widely separated in the trunk-region (*cf.* fig. 2), closely approximated in the ventral line in the caudal (fig. 3). The neural arches are at this stage first differentiated, in the form of bilaterally symmetrical upgrowths of the skeletogenous sheath (fig. 3, *n.a.*), separated by a wide interval in the mid-dorsal line.

Stage Q.—A transverse section through an intervertebral region at this stage shows that, concerning the skeletogenous sheath (*t.a.*, text-fig. 2 and Pl. I. fig. 6), the cells remain practically unchanged, their nuclei when examined under a high power presenting the oval contour indicative of mutual apposition, so characteristic of the earlier stage afore-described.

Comparison of a similar section through a vertebral region shows (text-fig. 3) that chondrification has there set in, but not at all points—for, while laterally hyaline cartilage is now present, in the form of paired masses (*c.v.*), continuous with the now cartilaginous neural arches (*n.a.*) and confined to the superficial layers of the

skeletogenous sheath, in both dorsal and ventral middle lines the latter (*s.s.*) has remained unchanged.

Comparison with the foregoing of a lateral longitudinal section at a slightly later stage, shows (Pl. 1. figs. 7 & 8, *c.v.*) that these lateral chondrites encroach upon the skeletogenous sheath from without inwards, rapidly involving its deeper layers, until its innermost limit is reached. They also effect the replacement of the afore-mentioned median portions, but by union within the deeper layers and subsequent extension in the opposite direction—*i. e.* from within outwards, as is seen at *c.v.* in Pl. I. fig. 6, which is that of a median longitudinal section at this period.

The above described processes continue until chondrification of the vertebral portions of the skeletogenous sheath is complete, and there thus results a metameric segmentation

Fig. 2.

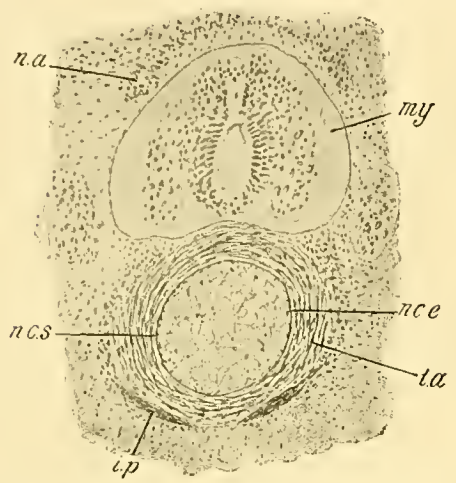
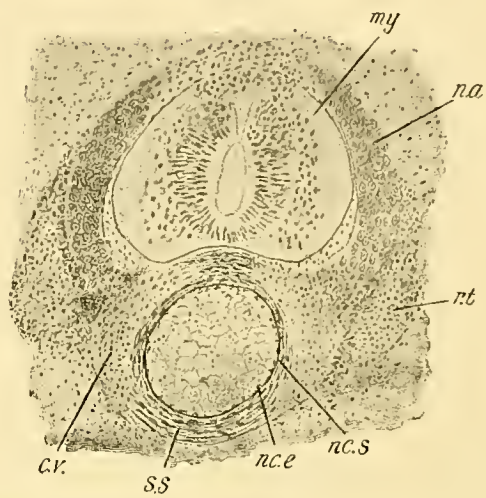


Fig. 3.



Transverse sections through the poststernal region of the trunk of *Sphenodon*. 2. Intervertebral; 3. Vertebral, drawn for comparison. Camera lucida × 70.

c.v. Cartilaginous vertebra; *i.p.*, primitive paired intercentrum; *my.*, myelon; *n.a.*, neural arch; *nc.c.*, notochordal epithelium: *nc.s.*, chordal sheath; *r.t.*, trunk rib; *s.s.* skeletogenous sheath; *t.a.*, inter-articular tissue (intervertebral portion of skeletogenous sheath).

of the vertebral axis, whereby a series of segments become recognizable, each comprising a centrum, an intercentrum, and a pair of neural arches; and the facts justify our regarding the centrum as of paired origin—a view which lends support to Gadow's conclusion that it represents the fused "interventralia" of the lower vertebrate forms.

As is well-known, the chevrons and præsternal or cervical intercentra present in most Lacertilia may, by shifting, come into secondary relationship either with the vertebræ in front of them [1] (by which they may even be carried down on autogenous hypapophyses, as in the neck of the Mosasaur Tylosaurus [2]), or with those behind

[1] *Ex.* Anguidæ, Varanidæ, Helodermatidæ; and, with eo-ossification, Mosasaurus, some Varanidæ, and Pseudopus. (*Cf.* Boulenger, P. Z. S. 1891, p. 113, and Gadow, Phil. Trans. vol. 187 B. 1896, p. 30).

[2] *Cf.* Osborn, H. F.: Mem. Americ. Mus. Nat. Hist. vol. i. 1899, p. 171; and also Americ. Nat. vol. xxxiv. 1900, p. 1.

them, as in Tupinambis [1]. This notwithstanding, since the anterior element of the whole series (that lying between the skull and first vertebra) is the first intercentrum, precision and uniformity are gained by enumerating it in correlation with the centrum behind it, and so on for the whole series which follow—as has been done, for example by Gadow, for the chevrons, though not with that uniformity which is desirable. The method mostly adopted, especially in illustrations, of associating with the numeral indicative of a given chevron that denoting the vertebra in front of it, as has been done with descriptions of the skeleton of the adult Sphenodon from Günther to Osawa, leads to confusion and must be given up.

Passing now to the intercentra, a marked advance is seen to have taken place in those of the anterior twelve body-segments and the tail. At Stage P the intercentral bodies are everywhere paired. At Q, fusion in the mid-ventral line has come about in the anterior region (*cf.* Pl. I. fig. 8, *i.p'.*). In the case of the first four bodies, the contour of the fused product gives no indication of its paired origin, but from the fifth to about the twelfth (as determined by very careful examination of serial longitudinal sections) a median depression remains. These facts are embodied in column Q of our table on p. 27, and perusal of them would seem to indicate that fusion of the paired intercentra takes place antero-posteriorly.

At Stage P, owing to the absence of demarcation between the cranial and vertebral portions of the differentiating tissues, the enumeration of the centra had to be determined by reference to the sacral region, *i. e.* the segments had to be worked out in postero-anterior succession. The numerous practical difficulties arising from this necessity, leave us in doubt whether the first and second intercentra are or are not represented at this stage. Hence the ? in our table, column P (p. 27). This consideration would seem to throw some doubt upon the paired origin of these first two intercentra; but, judging from the fact that from segments 12 to 5 the unpaired intercentra at Stage Q still show traces of paired origin, and that in segments 4 and 3 these elements are proved to be beyond doubt originally paired, we deem it fair to conclude that the same conditions apply to segments 2 and 1.

It may be remarked that at this stage (Q) the union of the first centrum with adjacent parts is effected. While it fuses (fig. 8 *a*) completely with the second intercentrum (*i.p'.*), it does so only peripherally with the second centrum, and that so as to enclose at * a central mass of undifferentiated tissue.

The neural arches have at this stage completely united in the dorsal middle line and are fully chondrified.

Passing to the caudal region, the intercentra of its fourth and succeeding vertebral segments, by an astonishing rapidity of growth, have acquired a characteristic elongation, each extending downwardly into (Pl. I. fig. 7, *i. p.''*) the substance of the tail, but without meeting its fellow. Although they are chondrified, and at this stage differentiated in advance of their homologues—the paired intercentra—in front, their cells

[1] *Cf.* Boulenger, G. A.: *op. cit.* p. 114.

are still more closely aggregated than those of the centra, wherefore they appear under the microscope dark and highly conspicuous.

Stage R.—This stage is most noteworthy for the completion of chondrification in the median plane (*cf.* Pl. II. fig. 11) of the vertebral bodies, throughout the whole length of the column, and for the lateral extension of these. Ossification of them has now set in, chiefly in the dorsal and ventral surfaces as seen in transverse section (Pl. II. fig. 11, *o.v.*). The neural arches begin to ossify independently of each other and the centrum, by an identical and similarly superficial process, as represented (for Stage S) at Pl. II. figs. 4–6.

At this stage a remarkable change, for which we were not prepared, is undergone by the intercentra of the segments numbering 11 to 29 (*i. e.* those between and including the third sternal and second caudal segments), viz., the complete disappearance of those belonging to segments 13 to 25 (*cf.* table, column R, p. 27); and the tendency to disappearance, to an extent which renders it difficult to identify their presence, for segments 11 and 12 and 26 to 29. We are unable to say at this stage by what process this removal is effected, whether by absorption into the intervertebral tissues or otherwise; but, in view of the discovery of this remarkable fact, it is the more astonishing to note that while one pair (viz. those of the third caudal segment) remain in their primitive condition, those which follow this in order of succession behind, while still unossified, have coalesced distally, enclosing the caudal canal, to form the so-called "chevrons,"—which are thus proved to be the direct derivatives of primary paired intercentra.

Stage S.—Viewed in median longitudinal section, the salient advances at this period are seen to be four in number. Firstly, the ossific tracts, described in the previous stage (Pl. I. fig. 10, *o.v.*), when viewed in transverse section (Pl. II. figs. 4 & 5), are seen to be extending into the lateral cartilaginous expansions, which are being rapidly absorbed over the areas marked †. Internally to these ossific centres and immediately surrounding the notochord, there are marked signs of calcification revealed by the selective action of our reagent. Exactly the same processes take place in the ossification of the centrum of the atlas (os odontoideum) as of an ordinary vertebra (*cf.* Pl. I. fig. 9 *a'*).

The advance in ossification of the vertebral bodies (*o.v.*, Pl. I. fig. 10) is seen to go on hand in hand with the assumption of a more truly hyaline character by those portions which are still cartilaginous. These (as viewed in longitudinal section) are seen at the same time to undergo a marked change in shape, becoming thinned over the centre of bony deposition and thickened at and towards their extremities—*i. e.*, an inverse development of bone and cartilage is recognizable, in proportion as the centre of each developing vertebra is approached.

In the intervertebral regions (*t.a.*, Pl. I. fig. 10) the cells of the skeletogenous sheath, still closely crowded, retain, in the elongation of their nuclei, a character originally

common to the whole sheath; but there has appeared around them a feebly hyaline matrix. The now clearly recognizable differences in the parts generally admit of the application of the term *interarticular tissue* to these intervertebral areas; and we desire to emphasize the fact that though they are feebly hyaline, "intervertebral disks" are not present—the hyaline matrix, dense and resistant for the vertebral bodies, diminishes markedly as the extremities of the centra are reached, and at these fades into the more flexible interarticular tissue, there being no hard and sharp line between the two.

The process of differentiation at this stage is most noteworthy for the full formation of an important constituent of the individual vertebra, which it so happens our reagents differentiate with startling effect. This, which we propose to term the *chordal plate*, is located transversely in the central and most constricted part of the developing vertebra. We have encountered it (Pl. I. fig. 10, *n.p.*) in all regions of the column, from the first (odontoid) vertebra (fig. 9) to well into the region of the tail. Microchemically, it reacts in a totally different manner to the reagents we have employed to anything else thus far described, wherefore there is no room for ambiguity concerning it. Its general matrix, which is extensive, stains a deeper blue than any other form of skeletogenous tissue which is present, and when examined under a high power its very conspicuous appearance is found to be due to the extent of its matrix and the presence of regular circular spaces, each filled by a cell which hardly stains at all and contains a conspicuous rounded nucleus. From its general appearance and disposition we have no doubt that it represents the so-called *chordal cartilage* described by Gegenbaur in 1862 [1] in the Urodela and Reptilia, and since observed by Field, Fraser, and Stöhr in certain allied forms and by Goette in the Anura.

Gadow has given (*op. cit.*) an admirable summary of the work of these investigators, all of whom regard this as chordal in origin, and of others who seek to disprove that. With the latter he is himself agreed. He deals with the question in full in Lacerta and the Geckos among Lacertilia, and since we are dealing with Sphenodon, it is with his statements that we are alone concerned in detail. Having referred (*op. cit.* p. 11) to an "occasional perforation of the elastica externa" in the Urodela, he is most emphatic as to the rending asunder and destruction of the chorda (p. 26) during the formation of the plate in certain Lacertilia. He describes this plate as a septum of which the cells "retain the appearance of young or embryonic cartilage." Dealing with the embryonic Lacerta, he asserts (p. 24) that he is "absolutely certain this so-called chordal cartilage . . . . . does not exist, if thereby be understood cartilage which is produced by the conversion of chorda cells; nor does this cartilage invade the chorda." His context shows this statement to be based mainly upon the examination of transverse sections, of which he says that they "allow the elastica externa to be traced as a continuous, unbroken line, which becomes irregularly folded, or creased, as

[1] Gegenbaur, C.: Untersuchg. z. vergleichd. Anat. d. Wirbelsäule b. Amphib. und Rept. 4to. Leipzig, 1862.

the sections approach the septum"; and he adds that "the cartilage of the latter is nowhere in direct contact with the cells of the chorda." The figures which illustrate his memoir are unfortunately diagrammatic, but that of a longitudinal section of the caudal vertebra of an adult Haplodactylus (p. 26), taken conjointly with the descriptive text and the associated remark that "in Phyllodactylus the chorda is only constricted," leaves little doubt in our minds that he would regard the chordal plate as ectochordal. We, on the other hand, are as emphatic to the contrary as concerning Sphenodon [1], since we are convinced that in that animal it is endochordal and intimately associated with the chordal epithelium in origin, as asserted by Gegenbaur.

It first appears at Stage R (Pl. II. fig. 11, *n.p.*) at the periphery of the chorda, and entirely within the chordal sheath, which by our method of treatment stains at all points light yellow as opposed to the blue of the chordal plate. On comparison of Stage S with R (fig. 11), it will be seen (Pl. II. fig. 12) that the plate increases by a process of inward proliferation. When at S it is worked out in detail in longitudinal section, two important facts are very evident, which are wholly irreconcilable with the theory of an ectochordal origin—viz., in the first place, that the tissue of which the plate is peripherally composed can be traced into continuity with the chordal epithelium, in a manner which suggests that it arises from this by special activity of its cells; and, in the second place, that its antero-posterior faces show no sharp line of demarcation from the substance of the notochord, but rather, on the contrary, a passage into it—the faces of the plate being irregular, and, as it were, sending prolongations of the matrix into the chorda (*cf.* Pl. I. fig. 10). The matrix of the plate is often seen to be feebly differentiated as its centre is reached, and in median longitudinal section a gradual transition into the central cells of the chorda may be observed [2].

Interesting, in consideration of recent discovery concerning the truncal origin of the amniote occiput, is the fact that at this stage there is present, wholly within the central tissues of the chorda (as it were in very testimony to the origin from this of the plate-tissue), a similar differentiation; and the fact that the distance between it and the chordal plate of the os odontoideum is about equal (*cf.* Pl. I. fig. 9, *n.p.*) to that between the latter and the plate next in order of succession behind. is not without significance. Going back to Stage R, we find this intrachordal mass represented by an essentially similar, though somewhat irregular, differentiation of the chordal epithelium, over the whole length of the intracranial notochord (Pl. I. fig. 9), with

[1] *Cf.* our footnote and reference to Zykoff, on p. 22.

[2] Dr. Gadow has courteously allowed us to compare his sections with our own. We can confirm his discovery of the ectochordal origin of the plates in Lacerta. His sections of Gecko, however, are in complete agreement with ours of Sphenodon. We conclude that the plates may arise in two independent ways; and we would accordingly distinguish between the Lacertan type in which they arise by inward extension of the skeletogenous tissues with accompanying constriction of the cuticular sheath (elastica) and the Gecko-Sphenodon type, in which they are chordal and lie at all stages within this. A most interesting result, but by no means without parallel in the animal kingdom.

accompanying indications of there having been a similar change in the general substance of the chorda and the adjacent tip of the odontoid vertebra.

The neural arches at this stage call for no special comment. Turning to the intercentra, a further suppression of the primary paired series has to be recorded—viz., that of the bodies related to segments 10 to 12 and 26 to 29, thus giving a condition of the complete absence of these between and including 10 to 29. With careful focussing the disappearing primary intercentra (the mode of removal of which we were unable earlier to determine) can be at this stage observed to lie wholly within the substance of the skeletogenous tissue (cf. *i.p.'*, Pl. I. figs. 9 & 10); and by comparison of the several segments we have convinced ourselves that their disappearance is not due to a process of absorption and decay, but to one which may best be described as a sharing in the progressive differentiation of the skeletogenous tissues—*i. e.*, there is no loss of substance, but merely a histological change, leading to a loss of individuality.

On the completion of this remarkable process, the intercentra are present only for the segments 1 to 9 and from the 30th backwards, *i. e.*, in precisely those regions in which in the Lacertilia they are most generally retained; and, as concerning the more precise limitations of this intercentrumless area, this comparison becomes more close as the development of Sphenodon advances—until a passing condition is reached in which, as regards its intercentra, the backbone becomes, as it were, that of a Lacertilian. The anterior intercentra remain unossified, but it is during this stage that the caudal ones (chevrons) ossify, and that as the result of a superficial deposit, which in its early condition, as is the case with the neural arches, forms a bony shell (*cf.* Pl. II. fig. 13, *i.p.''*, and figs. 4 & 5, *na.*). Owing to the rapidity with which this process is effected, we have not been able to ascertain whether ossification arises at more than a single centre.

Stage T.—The most conspicuous feature of this, the first stage after hatching, is the great extension of ossification and calcification, with accompanying constriction of the mid-vertebral areas and a general dawning of the adult characters. The process of ossification in the centra (*ov.*, Pl. I. fig. 13) has invaded all but the innermost two to three rows of cells, which are still but calcified; and it is densest at the point of greatest constriction. Both within the intervertebral areas (*t.a.*) and the central substance of the chordal plates (*n.p.*) calcification has become highly conspicuous, and in the case of the latter it extends into the processes afore-mentioned, which pass into the chorda-tissue.

The cells of the skeletogenous tissue which mark the boundary-lines between the intervertebral masses and the vertebræ have undergone a complicated rearrangement. These lines are delimitable by the fact that the nuclei of their cells, which are small, are vertically disposed in close aggregation, as compared with those of the central intervertebral series which are larger and run parallel to the longitudinal axis. Those

of the ends of the vertebræ, which during the earlier stages were structurally uniform with the cells adjacent, have at this stage become large and rounded, whereby their matrix is less conspicuous. Once again there are no structures recognizable which merit the term "intervertebral disks," nor is there any discontinuity of parts.

At this stage a still further numerical reduction of the primary intercentra goes on, their disappearance involving segments 5 to 9 and segment 30 (*cf.* table, column T, p. 27), leaving only four present in the præsacral region and traces of a fifth. The third, and probably the second and first, at the same time commence to ossify, which they do endogenously. For certain of the segments which have lost all traces of their primary intercentra, there now takes place the formation of an entirely new set of parts, remarkable no less for their time of appearance than for their detailed structure. These, which arise in relation to segments 9 to 13, appear wholly beneath, though in close apposition medially with, the interarticular masses (*t.a.*, Pl. 1. figs. 13, 14), but with them they have at first no sort of connection. Laterally quite free of them, they lie between them and a tract of coarse fibrous tissue which (*f.t.*) besets the ventral face of the vertebral column. Each of these *secondary intercentra* stains deep yellow, as does ordinary bone. The most remarkable character of them, however, is the presence of a very dark and deeply-staining central portion (*cf.* fig. 14), which is highly conspicuous under a high power of the microscope, and into which there pass convergently coarse fibres arising from the underlying tissue, which by their refractability are easy of observation and impart to the bodies a highly distinctive character. These secondary intercentra are from the first median and transverse, and in this they differ *in toto* from the primary, which arise in pairs.

Adult Vertebral Axis.—On the anatomy of this we have nothing that is general to add. Developmentally, the most noteworthy advances, apart from the mere completion of the vertebral bodies. notochordal plates, and chorda, concern the interarticular tracts (which have become more distinctly fibrous) and the intercentra (which now are finally present along the whole length of the vertebral column). The tail-vertebræ and their special peculiarities will be considered later.

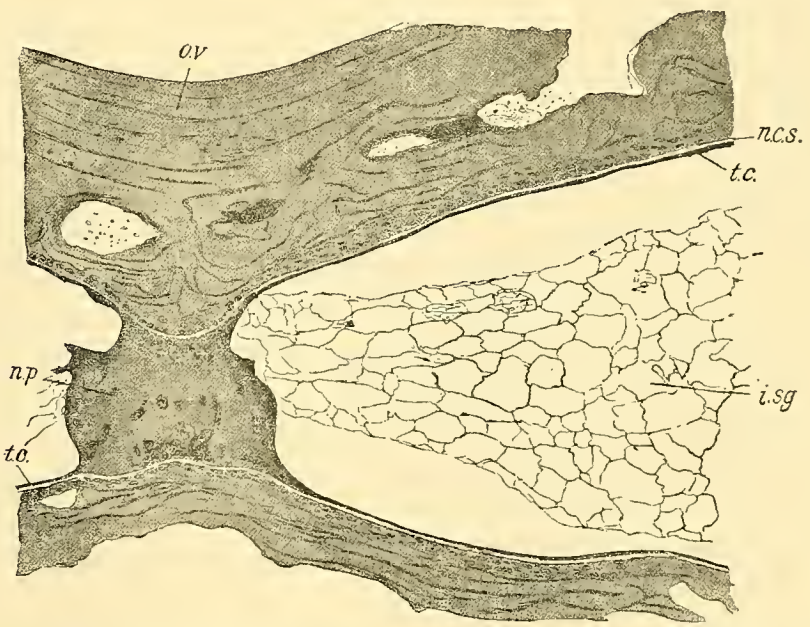
Goette has recently briefly described [1] the detailed structure of the fully-formed vertebra of Sphenodon, but that imperfectly, and judging by his figures from apparently none too well-preserved material. He omits mention of the chordal plate, and describes the chorda remnant as passing continuously through the vertebræ. He further remarks upon the peculiar constitution of the osseous tissue of the vertebra, which he regards as "no true bone," but rather to be compared in part to a poorly-celled calcified cartilage, with enclosed medullary nests, and of an exceptional type for the living Amniota.

We figure longitudinal sections from the sternal region of the adult backbone, stained with hæmatoxylin (Pl. I. fig. 15). The intervertebral tissues are now strongly

[1] Goette, A.: Zeitschr. wiss. Zool. Bd. lxii. 1897, p. 364.

fibrous, and on the ventral side they, together with the subvertebral fibrous tissue (*f.t.*), have attained to full differentiation. Their cells are arranged in parallel series, with an accompanying loss of individuality, the tissues having the appearance of being permeated by widely-separated parallel rows of small and elongated nuclei. While peripherally this parallel arrangement becomes more conspicuous, in the deeper layers the fibres become stronger, their attachments to the bony vertebræ appearing more marked, as the result of their greater avidity for the stain. Owing to the increase in thickness of the bony shell of the vertebral body (still largely composed throughout its inner moiety of calcified cartilage), the chordal plates (Pl. I. fig. 15 and text-fig. 4, *n.p.*) are comparatively insignificant as compared with the earlier stages. They are, however, present, and, owing to their completely septate nature, the chorda is now broken up into a series of elongated and recurrent interseptal segments, each of which is seen to be bounded not by the chordal epithelium hitherto recognizable, but by a deeply-staining and structureless cuticle, which passes into the faces of the plates, the superficial portions of which stain correspondingly with it.

Fig. 4.



Median longitudinal section of the adult vertebral column (caudal region) of *Sphenodon*, to show the tunica chordæ (*t.c.*) and its relationships to the chordal sheath and plate. Camera lucida, ×70.

i.sg., interseptal segment of chorda; *n.c.s.*, chordal sheath; *n.p.*, chordal plate; *o.v.*, osseous vertebra; *t.c.* tunica chordæ.

This cuticle, which we propose to term the *tunica chordæ* (text-fig. 4, *t.c.*), would appear to represent the chordal epithelium; but that it underlies and is independent of the chordal sheath (*nc.s.*) is proved by the fact that this stains lightly and can

therefore be easily traced and seen to be continuous along the whole length of the vertebral column. We have searched in vain for evidence of the "occasional breaking-down" of the cuticular sheath (cl. interna) in the vertebral regions as supposed by Zykoff for Siredon (Bull. Soc. Nat. Moscou, Bd. vii. 1893, p. 34).

The main cells of the chorda do not undergo any marked change, but in the centre of each interseptal mass, at the point coincident with that of greatest flexibility, there has now arisen, apparently by accumulation of a fluid contents, a conspicuous globular vesicle (Pl. I. fig. 15, *v.c.*), which we propose to term the *vesicula centralis*, and assume to be in some way associated with facilitating the movements of the parts.

Goette, by an ingenious argument, has drawn the conclusion (*op. cit.* p. 366), primarily from the study of the caudal region, that in Sphenodon the vertebræ are not truly amphicœlous. He extends this conclusion with qualification to the trunk-vertebræ, which he figures as transmitting an uninterrupted notochord. Osawa has adopted his view and applied it to the vertebral column generally (98[a]. p. 104). We defer consideration of the caudal region, which is specialized on its own lines, till later, but acceptation of Goette's view nevertheless depends entirely upon what we are to understand by an amphicœlous vertebra. As constituted in many bony fishes, this type of vertebra, at first sight solid, at its central and most completely constricted region, is in reality perforated by a minute aperture or *canalis dicentralis*, for transmission of a delicate thread-like process of the notochord connecting the adjacent inter-vertebral masses. If such be termed an amphicœlous vertebra, as is customary, the mere continuity of this notochord in Sphenodon would be no justification for disregarding the accustomed terminology under which its vertebræ are described as amphicœlous. If, on the other hand, by an amphicœlous vertebra be meant one centrally solid and with excavated extremities,—*i. e.*, a vertebra of which one or both articular faces have not become condylar or flattened—then the term may be applied to Sphenodon, the peculiar characters of its vertebræ being in this case the great depth of its concavities. Inasmuch as we have shown the chordal plates to be notochordal derivatives, we agree with Goette, in a sense, as to the presence of a continuous notochord, which on the whole simplifies the customary conception of the Rhynchocephalian vertebra. If, however, for argument's sake we dismiss the chordal plate with the rest of the chorda, the characters of the Sphenodon-vertebra become more nearly comparable to those of the cylindroidal type to which Credner has specially drawn attention in Palæohatteria (*op. cit.* p. 492), which may or may not have been plate-bearing. Viewed from this standpoint, the extension of Goette's argument by Osawa, instead of supporting his defence of the supposed Agamid affinities of Sphenodon, weakens it to an unexpected degree.

Passing now to the caudal region, the most important facts concerning the

vertebral axis (apart from outstanding processes and chevrons) lie in the study of the "splitting" phenomenon and the intervertebral chorda. Since the days of Cuvier, a good deal of interest has centred in the study of this process, by which the Lacertilian tail may be cast off. Hyrtl, Gegenbaur, Müller[1], and Leydig have more especially studied its details, which involve to a conspicuous degree the chordal plate, as Gegenbaur first pointed out. Gadow has recently summarized our knowledge of the nature and extent of the subdivision-line recognizable on the exterior of the vertebra capable of "splitting" among certain Lizards; and perusal of his statements will show that as to its position and relationships to the neural arch and transverse processes variability may be recognized, the "split" subdividing the vertebra in some cases into equal, in others into unequal portions. In Sphenodon this suture usually first appears on the caudal vertebræ numbering 6 to 8, and it may be present for all posterior to it. Günther, who first described it in Sphenodon, states (67. p. 606) that it "passes through the middle and behind the transverse process." Gadow, on the other hand, figures it as passing in front and subdividing the vertebra into approximately equal halves, of which the posterior bears both transverse processes and neural spine. With this we are in agreement (*cf.* Pl. I. fig. 18), but we have noted that while the suture may occasionally pass through the expanded base of the transverse process[2], it may also subdivide the neural spine (as in Pl. I. fig. 20) in a manner anticipatory of the more symmetrical division which, according to Gadow (p. 29, figs. 22 and 23), appears to involve the anterior neural spine[3] of Lacerta ocellata. And further, the characters of the first three suture-bearing vertebræ prove conclusively that although an elongation is effected when the suture is present, it is a subdivision and not a duplication which has taken place, since in vertebræ which are in all other respects identical with those immediately in front, the suture, which is restricted to the centrum in nos. 9 and 10, passes gradually up to the arch, assuming the condition characteristic of those behind.

We have noted that in the adult vertebral column both halves of the splitting vertebra send down minute but definite autogenous hypophyses, which have not before been described. These (*ha.'*, Pl. I. fig. 18), when examined *in situ*, are found (fig. 19) to extend into the walls of the hæmal canal, to which they act as extra supports.

[1] Müller, H.: Ueber Regeneration d. Wirbelsäule u. d. Rückenmarks b. Triton u. Eidechsen. 4to. Frankfurt, 1864. For other references, see Gadow, *op. cit.*

[2] We consider Cligny in error in his recent argument ("Miscell. Biologiques," Travaux d. l. Station Zool. d. Wimereux, tom. vii. 1899, p. 432), that the power of fracture and the "double pleurapophysis" are associated with ancestral characters. The probability that the centra of the Amniota are compounded of the "intraventralia" alone is completely opposed to it.

[3] So called by Cope in Dipsosaurus and Sauromalus, Proc. Amer. Phil. Soc. vol. xxx. 1892, pp. 202–205. Comparison with Sphenodon renders it extremely doubtful if this is a product of division, as assumed by Boulenger (P. Z. S. 1891, p. 169). We would rather regard it as a secondarily formed outgrowth like the autogenous hypapophyses which we herein describe.

Equally significant, as proving that the splitting phenomenon is secondary, is the fact, already pointed out by Gegenbaur in 1864, that the changes which render it possible appear as, by ossification, the vertebra is assuming the adult condition; and in support of this we are able to state that the bony centrum and chordal plate (both of which become split as the adult condition is realized) are in the developmental stages complete. The first appearance of subdivision is at Stage T. In fortunate sections of the adult we have been able to determine the probable method of splitting, and that it is, at least to a large extent, due to invasion of the bony vertebra and ultimately of the chordal plate itself (cf. *np.*, Pl. I. fig. 17) by the surrounding tissues, with accompanying absorption, since in sections in which the process was going on we find an inward extension of these tissues into the parts already ossified, with an accompanying peri-vertebral striation radiating from the split (*cf.* Pl. I. fig. 17, *x*.) such as we have encountered nowhere else. The bony vertebræ, however, continue to thicken after the first appearance of the split, and nowhere more so than at its opposite edges; wherefore it follows that by this, which is a growth process, the split is extended outwards.

We find in the intervertebral regions of the tail that a series of changes of a somewhat remarkable and intensely interesting order are undergone. Goette has recently described them in part. He calls attention (*op. cit.* p. 365) to the fact that in the caudal region the opposite ends of the vertebræ, which in the trunk are usually directed outwards, are inwardly thickened, and that they so constrict the vertebral canal that it is most spacious within the vertebra and narrowest at its extremities. In this respect the caudal vertebra presents a striking contrast with that of the trunk-region, in which the ends are widely open and the centre is contracted. He asserts that correlatively with this constriction an ingrowth of the intervertebral mass, already foreshadowed in the trunk-region, has effected a complete blocking of the intervertebral area, with accompanying segmentation of the chorda. When first examined, the intervertebral regions of the tail of a mature Sphenodon do appear to be compact, as Goette asserts; but when further investigated in well-preserved material the parts there present are seen to be complex, and to bear to one another a relationship essentially similar to that which the chordal plate bears intracentrally to the vertebral body. The interseptal chordal segment (Pl. I. fig. 17, *i.sg.*) becomes divided throughout its intervertebral region by a cartilaginous plate (*n.p.'*) lying wholly within the chordal sheath, continuous with the tunica chordæ, and having essentially the same structure and evidently the same origin as the chordal plate (*n.p.*). Indeed, the first indications of this are met with at Stage T, as a well-marked thickening of the tunica chordæ and its associated cellular tissue. As fully differentiated, this, which we propose to term the *intervertebral chordal plate*, in contradistinction to the chordal plate which is *intravertebral*, reveals terminal calcifications, and a centrally less dense area at the point where movement of the parts is greatest, which, while providing for the necessary flexibility, furnishes additional support. It would thus appear that under the weakening influence associated with the

splitting of the strongest part of the vertebral complex, a compensating development is deliberately initiated in the intervertebral—a process to which the term of Dohrn and Kleinenberg, "substitution of organs," may be not inappropriately applied; and beyond the extent to which these intervertebral plates may furnish support and be concerned in determining points of muscular attachment, we are inclined to regard the intravertebral plates as direct agents in the formation of the axis of the reproduced tail. This matter, however, requires further investigation. There remain only for consideration the definitive intercentra of the region of disappearance of those of the primary series, viz. segments 5 (?)–6 to 30. The intervertebral region of each of these shows an intercentrum of considerable proportions (Pl. I. fig. 15, *i.s.*). This, the *secondary intercentrum*, agrees with those already described (*antea*, p. 20) in lying outside the skeletogenous tissues, as figured by Goette (*op. cit.* pl. xvii. fig. 25, *x*). Not wholly so, however! The most distinctive character of these remarkable bodies is a sharp demarcation into a greater feebly-staining outer portion and a lesser inner one, which differentiates darkly and, when viewed in section, tapers into the intervertebral mass. The cells of their inner moiety are more numerous and much larger than those of their outer; and since in the mode of disposition these are linear with those of the intervertebral mass, they would appear to be derived from it. If this be so, these definitive secondary intercentra would appear to represent those to which we originally applied the term, but with a superaddition of parts derived from the intervertebral tissues. Be this as it may, their formation finally completes the series of intercentra, which are now present throughout the whole length of the column.

Typically these secondary intercentra arise singly, as median and transverse masses. In one case, however (*i.s.*, Pl. I. fig. 16), we have noted that for segments 12, 13, and 16 to 20 (7 in all) they are paired. Boulenger has drawn attention (P. Z. S. 1891, p. 170) to the existence in Lacerta ocellata of paired intercentra in the posterior sacral and anterior caudal regions, and Leydig has figured a similarly-paired condition of one of the præsternal intercentra of L. agilis (*op. cit.* pl. iv. fig. 53). In the absence of any knowledge of secondary intercentra in the Lacertilia, we conclude that while in both species the paired elements are of primary order, in our exceptional Sphenodon those of the post-sternal region, which are paired, would seem to be of secondary, and that these may therefore be variable as to their median or paired nature.

Comparison of the caudal region of Sphenodon with that of Lacerta ocellata as described by Boulenger would seem to justify the conclusion that in the chevrons primary intercentra are alone represented. We find, however, that in the case of the first 4–5 this is not wholly so. In the adult Sphenodon, these are characterized by the fact that their proximal ends are united, as pointed out by Dollo in 1883 [1], whereby they appear to overarch the caudal canal. Credner has confirmed this observation, and

[1] Dollo: Bull. Mus. Hist. Nat. Belg. tom. ii. 1883, p. 324.

with equal acumen has made it the basis (*op. cit.* p. 501) of determination of the isolated chevrons of Palæohatteria as median caudal.

Seeking the explanation of this overarching in Sphenodon, it occurred to us, having proved the chevrons proper to be permanent primary intercentra, that their united "proximal ends," being serial with our secondary intercentra, may be the homologues of those and that the anterior 4–5 chevons are therefore complex [1]. In support of this conclusion we would point out that at those stages at which the secondary intercentra are undeveloped (Pl. I. fig. 12 and Pl. II. fig. 13) the extremities of the chevrons in question are in no way united; and proof of its accuracy has come to us in a specimen belonging to the Dublin Museum, in which (Pl. I. fig. 21) the right half of the anterior chevron (*i.p.''*) and the overarching lobe (our secondary intercentrum) have remained distinct.

We append, in tabular form (p. 27), a synopsis of the complicated series of changes undergone by the successively formed sets of intercentra; and in conclusion desire once again to emphasize the fact that in the most fully differentiated state the bony vertebræ and the fibro-cartilaginous interarticular masses of Sphenodon are organically continuous.

We are constrained to do this as Cope more particularly [2], and Gadow, though with greater caution [3] (reading as we believe theory and expectation into fact), have referred to the intervertebral masses in terms applicable only to discontinuous skeletal parts.

The so-called "Pro-atlas."—The most recent view expressed as to the morphology of these debateable elements is that of Gadow, who (*op. cit.* pp. 12, 13, and 37) has come to regard them as parts of the atlas—the serial homologues of his "supradorsalia" of the supposed ancestrally composite vertebra. In the conclusion that the atlas was thus originally more complex than has hitherto been supposed, and that the atlas and "pro-atlas" represent one vertebra, he has been followed by Osborn (*op. cit.* p. 173), who, from the study of the palæontology of the Reptilia, has come to regard the atlas as composed of five pieces and "persistently rhachitomous." Despite all attempts to discover facts which might help further to elucidate this question, we have failed. Appeal to the nerves availed us nothing, and all that we can add is that the "pro-atlas" so-called is præformed in paired cartilages (Pl. II. fig. 3, *p.a.*), which at Stage Q arise independently of both the cranium and the rest of the vertebral column, and are imbedded in the tendons of the dorsal skeletal muscles, near the point of attachment of these to the exoccipital, and that their articulation upon the skull is secondarily acquired (*cf.* Howes, 90, p. 357).

[1] We fully concur in Boulenger's refutation (Ann. & Mag. Nat. Hist. ser. 6, vol. xii. 1893, p. 60) of Dollo's hypothesis that "hæmapophyses are homologous in all Vertebrata."

[2] Cope, E. D.: Trans. Americ. Philos. Soc. vol. xvi. 1886, p. 248.

[3] Gadow, H.: Phil. Trans. vol. 187 B. (1896), pp. 33 & 51. The term "intervertebral disks" is apt to create the impression of existence of independent elements.

		P.	Q.	R.	S.	T.	Adult.
Cervical.	1.	?	*U.*	*U.*	*U.*	*U.*	*U.*
	2.	?	*U.*	*U.*	*U.*	*U.*	*U.*
	3.	*P.*	*U.*	*U.*	*U.*	*U.*	*U.*
	4.	*P.*	*U.*	*U.*	*U.*	*U.*	*U.*
	5.	*P.*	*U.* †	*U.*	*U.*	?	?
	6.	*P*	*U.* †	*U.*	*U.*	—	*F.*
	7.	*P.*	*U.* †	*U.*	*U.*	—	*F.*
	8.	*P.*	*U.* ↓	*U.*	*U.*	—	*F.*
Trunk.	9.	*P.*	*U.*	*U.*	*U.*	*F.*	*F.*
	10.	*P.*	*U.*	*U.*	—	*F.*	*F.*
	11.	*P.*	*U.*	?	—	*F.*	*F.*
	12.	*P.*	*U.*	?	—	*F.*	*F.*
	13.	*P.*	*U.*	—	—	*F.*	*F.*
	14.	*P.*	*P.*	—	—	—	*F.*
	15.	*P.*	*P.*	—	—	—	*F.*
	16.	*P.*	*P.*	—	—	—	*F.*
	17.	*P.*	*P.*	—	—	—	*F.*
	18.	*P.*	*P.*	—		—	*F.*
	19.	*P.*	*P.*	—		—	*F.*
	20.	*P.*	*P.*	—		—	*F.*
	21.	*P.*	*P.*	—		—	*F.*
	22.	*P.*	*P.*	—		—	*F.*
	23.	*P.*	*P.*	—		—	*F.*
	24.	*P.*	*P.*	—		—	*F.*
	25.	*P.*	*P.*	—	—	—	*F.*
Sacr.	26.	*P.*	*P.*	?	—	—	*F.*
	27.	*P.*	*P.*	?	—	—	*F.*
Caudal.	28.	*P.*	*P.*	?	—	—	*F.*
	29.	*P.*	*P.*	?	—	—	*F.*
	30.	*P.*	*P.*	*P.*	*P.*	—	*F.*
	31.	*P.*	*P.*	*Chev.*	*Chev.*	*Chev.*	*Chev.*—*F.*
	32.	*P.*	*P.*	*Chev.*	*Chev.*	*Chev.*	*Chev.*—*F.*
	33.	*P.*	*P.*	*Chev.*	*Chev.*	*Chev.*	*Chev.*—*F.*
	34.	*P.*	*P.*	*Chev.*	*Chev.*	*Chev.*	*Chev.*—*F.*
	35.	*P.*	*P.*	*Chev.*	*Chev.*	*Chev.*	*Chev.*
		↓	↓	↓	↓	↓	↓

Fig. 5.—Tabular statement of the order of arrangement and succession of intercentra for Stages P to T and the adult.

P. Primary paired intercentra. *U.* Unpaired intercentra of primary order. — Intercentra absent. *F.* Secondary intercentra. *Chev.* Chevrons. † Medially constricted.

Ribs and Sternum.—Ribs were attributed by Günther to the segments between and including the fourth præsternal (cervical) and the second sacral. Discriminating between the osseous rib as a "pleuropophysis" and its unossified ventral portion as a "hæmapophysis," he further distinguished between those vertebræ in which the latter is fully developed as "dorsal" and those in which it is reduced as "cervical" and "lumbar" respectively.

For the caudal region he describes the presence of "transverse processes" and

rightly records a transverse disposition of the first and second and the forwardly-directed one of those which follow (*loc. cit.* p. 606). In attributing the first cervical rib to the fourth vertebra he was in agreement with Owen, who first discovered this [1]. Baur, however, later described in an individual specimen the presence of a free rib upon the third vertebra, and showed at the same time that (86[c]. p. 736) the so-called caudal "transverse processes" of the adult represent co-ossified ribs. Osawa (98[a]. p. 485) declares his inability to confirm the presence of the latter; but, with Gadow, we can do so, and can confirm the occasional presence of a rib to the third præsternal vertebra. Neither Gadow nor Baur state the number of caudal ribs observed. Our own investigation shows them to be present (Pl. I. fig. 12) for at least the eight anterior caudal vertebræ. Posteriorly to these, according to Günther, the "transverse processes" become rudimentary, and we have no material to prove whether they do or do not ossify separately. The osseous rib-formula may accordingly now be rendered as follows, allowing for the possible presence of additional caudal ribs yet to be discovered:—

Præsternal	5–6
Sternal	3–4
Poststernal	13–14
Sacral	2 with variation.
Caudal	8 observed at Stage S.
Average	33

In the adult animal the anterior præsternal ribs alone stand related to both intervertebral and vertebral bodies (*cf.* Pl. II. figs. 1 & 2), the rest either articulating or, as in the case of the caudal and apparently in individual cases of the last three poststernal, becoming co-ossified with the vertebræ alone. Baur, in describing the præsternal ribs, has drawn attention to the existence of supposed ligamentous homologues in relation to the first and second vertebral segments, and to the third where an osseous rib is absent. Of these ligaments, he describes the first as single-headed and attached to the first intercentrum, the second and third as double-headed and attached to both intercentrum and transverse process of their corresponding vertebræ (*i. e.* those behind), and he points out that in its attachment to the intervertebral body the lower ligamentous tract agrees with the capitulum of the rib borne upon the fourth vertebra, which he, with Owen and Günther, describes as two-headed. Of the fifth rib, he rightly points out that it is the capitulum which is reduced, wherefore it follows that if his identification of these ligamentous tracts as vestigial ribs is correct, the first and fifth are diversely modified.

We can confirm (*cf.* Pl. II. fig. 2) the general accuracy of his description and

[1] Owen, R.: Cat. Osteol. Series R. Coll. Surgeons Mus. vol. i. 1853, p. 142.

can extend his discovery of an osseous rib for the third vertebra to an individual of Dendy's Stage S (Pl. II. fig. 1) and to adult specimens in the R. College of Surgeons and British Museum. If his "ligamentous ribs" are really such, it is reasonable to suspect that at some developmental stage they may be either definitely skeletogenous or may show traces of their supposed skeletal origin. After careful search, we are only able in support of this conclusion to point to the existence within the third ligament of an individual of Stage S of an insignificant cartilaginous nodule. The fact that no trace of a corresponding nodule was forthcoming in the two specimens of Stage R examined, leads us to regard the afore-mentioned case as an individual one of the presence of a vestigial rib.

Concerning the relationships of these supposed ligamentous ribs, there is a detail not recorded by Baur. As viewed at first sight (fig. 2), the double attachment would seem suggestive of a two-headed rib; but, in the case of the most distinctly two-headed osseous rib (viz., that of the fourth præsternal segment), the osseous capitulum and the supposed ligamentous one coexist, while for both this rib and those behind it, in which the capitulum is unrepresented in bone, the supposed ligamentous portion of the rib, instead of passing into the substance of the osseous one, as should be the case were it a constituent of the rib, merely skirts the lower border of that with an accompanying attachment of its fibres. Throughout the region of insertion anteriorly of the muscles termed by Osawa "costo-cervical," it leaves the rib and passes on as an independent structure, in the manner delineated in Pl. II. fig. 2, *m.'*—in exactly the manner which would result from an intimacy of mechanical relationship. When to this is added the disproportionate development of the first of the so-called "ligamentous ribs," which is in reality for the most part a muscular mass, we doubt how far these structures really represent ribs wholly or in part, and confess ourselves unable to definitely decide the question either way [1].

Turning now to the rest of the præsacral ribs, as concerning their heads and articulations alone, we find as we pass back from the fifth cervical the distinction between tuberculum and capitulum becomes gradually lost. With this simplification there takes place a reduction of the transverse process, which, never strong, disappears in the anterior sternal region, and, as pointed out by Osawa (98[a]. p. 735), is formed by

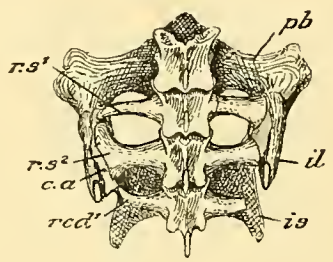
[1] At the outset of our investigation into the "cervical" region, mindful of the belief in the Cheloniau affinity of Sphenodon and the assertion by W. K. Parker ('Challenger' Reports, Zoology, vol. i. pp. 47 & 50) that in the embryo of the Green Turtle the somatomes of the neck and tail are more numerous than later, and undergo numerical reduction by abortion, we kept a look-out, in vain, for probable evidence of a similar process, so far as it might involve the skeleton in Sphenodon, in the hope of being able to obtain some clue to the meaning of the numerical variation of the reptilian præsternal segments so conspicuous among the Dolichosauria and Mosasauria. From the discovery of facts concerning the variation in relationship of the sternum which we herein describe (*infra*, p. 34), we are disposed to regard numerical variation among the præsternal vertebræ, if not the poststernal also, as associated rather with a shifting of the sternum than an excalation of segments, as Parker's allegation would seem to suggest.

both the centrum and the arch. Günther describes the heads of the ribs as "low and compressed," and attributes to them a wholly central articulation. Baur has more correctly shown (86. p. 735) that the connection is rather with the arch, but he nevertheless insists that "in reality the rib never completely forsakes the centrum."

We can confirm the details of Baur's description and extend them to Stage S.

Of the so-called "lumbar" ribs, *i. e.*, the posterior two to four of the præsacral series, the head of the last one may show increased expansion, and in this way that may become in a sense transitional to the sacral rib, the special feature of which (Pl. II. fig. 5, *r.s.*) is its general robustness and greater attachment to the centrum. Except to point out that the sacral ribs are ossified in the manner of the præsacral (Pl. II., *cf.* figs. 4 & 5), we have nothing to add to recorded descriptions concerning them. There are usually two pairs, of which the anterior are the more slender and transversely disposed, the posterior the more robust and forwardly directed (Pl. I. fig. 12, *r.s.*). The iliac articulation is usually furnished by their united outer cartilaginous extremities.

Fig. 6.



Sacrum with hip-girdle of an adult *Sphenodon*, bearing on the left side an abnormal set of ribs.

c.a., articular cartilage; *il.*, ilium; *is.*, ischium; *pb.*, pubis; *r.cd.*[1], first caudal rib; *r.s.*[1], *r.s.*[2], sacral ribs. Nat. size.

In view of the frequent existence of three sacral ribs in many living Lacertilia [1], of more than two in the Chelonia, of the occasional presence of a third in recent Crocodilia[2], and particularly of that of at fewest three pairs in Palæohatteria[3], interest attaches to a skeleton preserved in the Dublin Museum of an adult Sphenodon (text-fig. 6) having on the left side a trisegmental sacrum, on the right a sacrum and hip-girdle normal in all respects. The third sacral rib on the left (*r.cd.*[1]) is seen to be the first caudal, enlarged and expanded. Externally it was in life continuous by its outer

[1] Stellio and Chamæleo, Credner, H.: *op. cit.* p. 505. Phrynocephalus, Cope, E. D.: Proc. Amer. Philos. Soc. vol. xxx 1892, p. 207. For other examples *cf.* Siebenrock, F.: Ann. naturhist. Hofmus. Wien, Bd. vii. p. 373, and Sitzb. Akad.Wiss. Wien, Bd. civ. p. 67.

[2] Baur, G.: Zoolog. Anz. Bd. xii. 1889, p. 240.

[3] Credner, H. *op. cit.* p. 505.

cartilaginous border with that of the second sacral rib. This was stouter than usual, while the first rib, reduced externally to a degree proportionate to the extension of the first caudal into the sacrum, was reduced to the calibre of a præsacral rib. The combined cartilaginous heads of the three ribs, by union, furnished the iliac articulation, and there can be no doubt that the determining cause of this abnormality was the backward rotation of the left ilium, well marked. It may be a case of "vertebral assimilation" [1], but its interest is none the less if so.

We have only to add, concerning the caudal region, that at Stage S, when ossification is setting in, the detailed relationships of the caudal rib to its centrum and arch are closely identical with those of the sacral vertebræ (*cf.* Pl. II. figs. 5 & 6), and that at this stage comparison with the præsternal region (fig. 4) shows that the interarticular tissue between the rib and its vertebra is far less differentiated than there.

The most conspicuous difference recognizable on a survey of the whole series of rib-heads in the adult and the later developmental stages of Sphenodon, is the fact that while the individual rib is for the most part obliquely attached or articulated upon the anterior end of its related centrum, in the case of the third and fourth præsternal ribs, which are two-headed, this antero-ventral extension is more marked and involves the intercentrum, the capitular head abutting against that. For this an explanation has to be sought.

Examination of the posterior trunk, sacral, and tail vertebræ, at the period of chondrification, would seem to indicate (*cf.* figs.) that the ribs arise only in relation to the vertebral bodies, and that they may be derivative of either their arch system, as originally believed for the higher Vertebrata by Gegenbaur, Goette, and others; or of their transverse processes, as argued by Claus, and more recently by Corning [2] and others—*i. e.*, that in any case they would appear to be vertebral in origin, as has been more recently maintained for the ribs of the Vertebrata generally by Dollo [3]. Hofmann, in a memorable paper published in 1878 [4], from the study of both the anatomy and development of adequate representatives of all the amniote classes but birds, deduced the final conclusion that the ribs of these animals are primarily intervertebral. Baur has further sought to support this view [5], and Gadow, among most recent investigators, has done likewise, in his final conclusion (96. p. 50) that the ribs of the Amniota are lateral outgrowths and the chevrons and hæmapophyses ventral outgrowths of his "basiventralia," which give rise to the intercentra [6].

[1] *Cf.* Siebenrock, F.: Ann. naturhist. Hofmus. Wien, Bd. vii. 1892, p. 373.

[2] Corning, H. K.: Morph. Jahrb. Bd. xvii. 1891, p. 611; *cf.* also Goeppert, *ibid.* Bd. xxv. 1897, p. 247.

[3] Dollo, L.: Bull. Sci. Fr. & Belg. tom. xxiv. 1892, p. 113. For other references, see Hofmann, *infra*.

[4] Hofmann, C. K.: Niederld. Archiv, Bd. iv. 1878, p. 199.

[5] Baur, G.: Amer. Nat. vol. xxi. 1887, p. 942.

[6] Psychologically interesting in this association is the conclusion of Dollo (*op. cit.* p. 128), who, though apparently in error concerning the vertebral origin, regards the "ribs" as dorsal ribs, the "hæmapophyses" as ventral.

On examination of transverse sections through the developing vertebral column of Sphenodon at Stage P, at which the parts of the cartilaginous vertebræ are as yet undifferentiated, the tissue giving rise (Pl. I. figs. 3 & 4) to the paired intercentra (*i.p.*)—which, it will be remembered, are the first, and at this stage the only components of the vertebral column recognizable—is seen to be continuous with that differentiating into the ribs (*r.cd.*). Figs. 3 and 4 represent the first and sixth sections across an individual caudal segment; and comparison of those which intervene has shown us that even here, when the vertebral body is not yet differentiated, the disposition of the proximal end of the rib is oblique, involving ventrally and anteriorly the intercentrum, dorsally and posteriorly the region of the future centrum and arch. Comparison with the adult cervical rib reveals a close similarity of relationship; and since with later development the connection with the intercentrum is lost, the primary relationship of the rib is proved to be intervertebral.

Cope in 1878 first drew attention [1] to the existence in certain Permian Pelycosauria of a two-headed condition of the rib, with accompanying intercentral articulation of the capitulum; and Baur, eight years later, in his afore-mentioned paper on the cervical ribs of Sphenodon (prompted by Cope's announcement), sought to emphasize the importance of this. Cope, immediately afterwards, in dealing with the structural resemblances between these creatures, prompted by Hofmann's brilliant generalization afore-mentioned, penned the remarkable paragraph [2]: "The passage of time has seen in the Reptilia generally" a modification "in the mode of attachment of the rib," in which, "in passing from front to back, the intercentral articulation is lost, and finally the head of the rib disappears." The facts we have just described render this well-nigh prophetic; and it remains to be ascertained how far the supposition, deduced from the study of longitudinal sections alone, that the ribs of the Amniota, and of the Reptilia in particular, arise in exclusive relationship to the transverse process, centrum, or arch, will stand the test of examination in other planes, and, as deduced from that of developmental stages at which chondrification is more or less advanced, will bear further comparison with the earlier ones of procartilage differentiation.

Concerning the bodies of the ribs, we have nothing to add to the descriptions of Günther, Maurer (96), Osawa, and others, except as regarding the so-called "uncinate processes." Günther in his original description accords the first of these to the last præsternal rib, Osawa to the penultimate, but neither state their posterior limitations. Like those of the Ratite birds, they are apt to be easily lost in maceration; but in carefully prepared specimens we have been able to trace them back, with

[1] Cope, E. D.: Proc. Amer. Philos. Soc. vol. xvii. 1878, pp. 518 *et seq.*; and Proc. Amer. Assoc. Adv. Sci. 1884, pt. ii. p. 474.

[2] Cope, E. D.: Trans. Amer. Philos. Soc. vol. xvi. 1886, p. 249.

progressive diminution in length, to the 11th–12th poststernal rib. They are longest throughout the middle of the series, and they arise late at Stage Q, after the ribs have become chondrified, by independent concentration of the cells which go to form the intermuscular septa. They also chondrify independently at Stage R (Pl. II. fig. 7, *u.p.*), at which the ribs are well ossified. Jeffery Parker has already called attention [1] to their similar independence in Apteryx, and we accordingly follow him in the usage of the term *uncinates*.

There can be no doubt that the process borne by the last præsternal rib is a true uncinate, since our sections at Stages Q and R reveal its independent origin. We find that the "process" borne by the penultimate rib, which Günther (67. p. 607) believed to be homologous with the uncinates and which Osawa definitely refers to them, may by elongation assume the size and shape of one in its most pronounced form, as contrasted with its condition described by Günther of a mere "dilated hæmapophysis." On the study of this he was led to regard the uncinates as hæmapophysial in origin, "separate and removed from the distal end of the pleurapophyses as the latter increase in length." At our Stage R, at which the ribs are beginning to ossify and the uncinates proper are still distinct from them, the penultimate rib and its supposed uncinate are continuous, while a similar but feebly developed process is present on the antepenultimate rib. At the period of continuity, the penultimate rib and process may in some sections present appearances suggestive of a possible precocious union; but, inasmuch as we are unable definitely to detect its presence at an earlier stage or in a wholly free state, we leave it an open question whether the "process" may or may not be a mere outgrowth of the cartilaginous rib. If the non-extension of the osseous rib into the uncinate zone be due to loss of connection with the sternum, the former conclusion would be the more likely; if, on the contrary, it be not so, it may well be that, under the extension of the unossified moiety into the zone, the plastic cartilage has been seized upon as available for extension and support under the mechanical conditions at work.

The Sternum.—By way of descriptive detail, of the adult sternum we have nothing to add to the statements of Günther and Osawa, except to state that neither has recorded the fact that even in the adult its posterior border is notched. At Stages R and T this notch (Pl. VI. figs. 5 & 6, *s.n.*) is very conspicuous, and inasmuch as at Stage Q the two halves of the sternum are widely separated, the question arises whether or not the notched region is one of non-union of its opposite halves.

Parker, in describing the developing sternum of Apteryx, in the adult of which there are four pairs of sternal ribs, has shown [2] that the two anterior of these apparently give rise to the sternum, and that the connection of this with the two posterior is secondary and due to extension of both sternum and ribs. In Sphenodon three pairs

[1] Parker, T. J.: Phil. Trans. 1891 B, p. 80.

[2] Parker, T. J.: *op. cit. cf.* pp. 87 & 113.

of sternal ribs have been hitherto described for the adult, but we find that four pairs may be present, as, for example, in a skeleton in the Teaching Collection of the R. College of Science, Dublin. Similarly, in the developmental stages, four pairs may occur, as at Pl. VI. fig. 6 (Stage T), or four on the left side only, as at Pl. VI. fig. 5, or on the right, as in specimens of Stage S in our possession.

The earliest developmental stage of the sternum we have observed is at Q. In the section of this figured (Pl. VI. fig. 4) but two ribs are seen to contribute to the sternum, but examination of serially related sections proves that the third enters also into its formation; and, from what we have seen, we incline to the belief that when a fourth is present it also has contributed.

In the latest stage figured, the organic continuity between ribs and sternum is still uninterrupted, the "incisuræ costæ" being of late origin. As early as Stage R the sulcus coracoideus (*cor.*') is well indicated, and anteriorly the sternal plate is prolonged into a couple of episternal cornua, which skirt the stem of the interclavicle and contribute to the formation of the sulcus, in a manner which holds good for the adult, but has been inadequately recognized in all previous descriptions.

In the specimen from the Dublin Museum, this last right præsternal rib reaches the sternum, and its cartilaginous segment, by elongation and enlargement, has the characters of a normal sternal member. Its osseous segment is normal, and there are no accompanying changes recognizable in the ribs in front of it. We have already adverted to one point of interest attaching to this specimen (*antea*, p. 30); and if, as there is reason to believe from what is known of the Mesozoic reptiles, the amniote sternum in its ancestral condition, in which it was most certainly cartilaginous, was more extensive than its more specialized homologue of the living forms [1], fluctuation anteriorly and posteriorly such as we have recorded becomes the more readily intelligible.

There are no indications of any elements, median or otherwise, entering into the composition of the sternum, beyond those derivative of the ventral extremities of the ribs.

The "Abdominal Ribs" (Gastralia [2]).

These are in number 22 to 26, and they are alternately attached to the ventral segments of the poststernal ribs and free, at any rate for the most part, as originally pointed out by Günther. Osawa records 24, of which he remarks the first is attached to the first poststernal rib (98. p. 491), as are those behind corresponding to odd numbers, back to the 21st. The 22nd, 23rd, and 24th, with those corresponding to even numbers, he describes as free. We find, however, that regarding the first point there

[1] Osborn has described fossil an expanded cartilaginous sternum arising from ten pairs of ribs in the Mosasaur Tylosaurus dyspelor (*op. cit.* [*antea*, p. 14] p. 180).

[2] Baur, G.: Anat. Anz. Bd. xiv. 1897, p. 150.

is considerable variation. Boulenger has called attention[1] to the fact that "the anterior extremity of the plastron overlaps the posterior extremity of the sternum," and concerning this, two specimens we have examined yield interesting results. In each of them there are two free gastralia in front of the first that is attached to the ribs; and while in one example (that possessed of four pairs of sternal ribs) these are short and median, in the other (that in which the last "cervical" rib is sternal) the anterior gastralium is represented by a symmetrically-arranged pair of rods.

Günther originally described each gastralium as of three elements, and their natural relations are generally those indicated in Pl. II. fig. 10, no. 7. Not unfrequently union in the middle line, as figured and described by him, may occur, and it would seem to involve a forwardly-directed spur on the median element which is generally present (*cf.* Pl. II. fig. 10, no. 11). Much interest attaches to Günther's description of an exceptional specimen, in which for the rib-connected gastralia the lateral elements were attached to the central by transverse "joints," instead of being in oblique juxtaposition with them as for the free gastralia and as is more generally the case throughout the entire series. The fact that, in most specimens we have examined, individual gastralia of both the attached and free order show both "jointing" and juxtaposition, and that while in most cases one or two such "joints" may be present only on one side—there being no regularity recognizable,—proves that no physiological significance is to be attached to these variations.

Turning to the embryo, we find that the gastralia arise at Stage S, within previously differentiated fibrous tracts of the subcutaneous tissues of the body-wall (*g.t.*, Pl. II. fig. 9), by a process of calcareous deposition, which proves them to be wholly membranous in origin. Their connection with the myocommata of the body-wall is fully established later, and with Gadow[2] we have failed to detect any traces of a cartilaginous origin, believed by Schneider to be the case for the Crocodilia. Figs. 8 and 9 represent (8) the anterior (third to fifth), 9 the posterior (16th to 18th and more highly magnified) gastralia of an example at Stage S. It will be observed that the median element is present only anteriorly, and that while for two of the three segments figured comparison with the adult shows its lateral cornua to be partly represented by a series of minute calcifications, for the anterior segment it is composed of two pieces. Anteriorly the lateral elements are seen to be fully formed, but on passing to the posterior series two of the three figured are observed to be represented by a linear series of distinct calcifications, the median element being undeveloped. The fact that in the adult the gastralia which occupy the positions of those here figured are alike symmetrical and only trisegmental, proves that with advancing development a union of the calcifications such as are here figured must occur, and that the median elements

[1] Boulenger, G. A.: Brit. Mus. Cat. Chelonia, Rhynchoceph. & Emydos. 1889, p. 1.

[2] Gadow, H.: Morphol. Jahrb. Bd. vii. 1882, p. 77.

arise antero-posteriorly. It further indicates a compound origin for all the parts, median and paired alike; and concerning the anterior paired segments, which in the individual figured were single, we find that in younger individuals at the same stage they may be represented by a series of elements. The details point to the conclusion that union is rapid and irregular.

A striking characteristic is this irregularity of calcification! It leads to irregularity of union; and it is fair to assume that in this lies the explanation of the asymmetry which the parts of the adult "plastron" are apt to assume. It explains the not infrequent presence of but a single asymmetric element, and of so extraordinary a condition as that of the triradiate or quadriradiate union delineated on Pl. II. fig. 10 (Stage T)—the most erratic we have observed. It also renders clear the substitution of transverse "joints" between, for oblique juxtaposition of, the median and lateral elements described by Günther, and the co-existence of these herein recorded, while it presupposes other combinations yet to be discovered.

Interesting and unexpected as are these details ontogenetically, we have come to attach a still greater importance to their probable phylogenetic significance.

One of the most distinctive characters of Credner's Palæohatteria of the Permian is the multisegmented condition of its "abdominal ribs," which, on careful examination of the originals, he has shown to be also the condition in Von Meyer's famous Proterosaurus and other genera to which he refers (*op. cit.* p. 538). In view of the obvious similarity to the embryo Sphenodon suggested, it becomes the more interesting to find that whereas in Palæohatteria, according to Credner's original description, there appear to have been three rows of calcifications present for each rib, in Proterosaurus there were two or three. In a later paper, however, on Kadaliosaurus, an allied genus, he gives[1] the number of "abdominal ribs" as regularly six for each vertebral segment possessed of them; and in instituting comparisons with Palæohatteria, Proterosaurus, Stereosternum, and Hyperodapedon, he gives the number present in them collectively as from three to six. The calcifications in all these forms are regular and structurally constant, whereas in Sphenodon they are developmentally irregular and inconstant.

Kadaliosaurus is further interesting in the light of the foregoing observations upon the substernal extension of the "gastralia" in Sphenodon, as in it they are still more nearly pectoral in extent and Stegocephalian. The facts suggest that the "plastron" may be undergoing reduction in the living genus, a consideration which may perhaps explain the irregular mode of calcification by which it is formed.

Boulenger, availing himself of these facts of palæontology, has made them a basis of classification of the Rhynchocephalian Order to which we alluded at the outset (*antea*, p. 3), and he has drawn a sharp distinction between the higher suborder of the Rhynchocephalia vera (91. p. 171) (Hatteriidæ, Homeosauridæ, Rhynchosauridæ,

[1] Credner, H.: Zeitschr. deutsch. geolog. Gesellsch. Bd. xli. 1889, p. 330.

and Sauranodontidæ), characterized by the triserial condition of the "abdominal ribs," and the lower or Proterosauria (Palæohatteriidæ, Proterosauridæ, and Champsosauridæ), in which their segmentation is multiserial. The adult Sphenodon, if classified by its "plastron," can only be referred to the former—the developing Sphenodon might with justice be relegated to the latter and lower suborder! In this, Boulenger's far-sighted classification receives welcome support.

Moreover, the multisegmented condition of the "plastron" segments is nothing short of a Stegocephalian character.

The Skull and Visceral Arches.

In compliance with passing custom, we have adopted in this section of our work the reconstructional method, as before stated (*antea*, p. 7).

Beyond the memoirs of the late Kitchen Parker, and some recent preliminary notes by Gaupp, together with the observations of Leydig (*op. cit.*), Born, and Hofmann, duly mentioned by him, little has been written upon the actual development of the Lacertilian chondrocranium [1]; and since in the absence of figures we find it difficult to follow the details of Gaupp's descriptions, we deem it more prudent to describe connectedly the processes taking place in Sphenodon, which are simple and straightforward, and highly instructive in themselves.

The Chondrocranium.—In Sphenodon the cartilaginous elements of the skull arise before those of the greater part of the vertebral column, and the ossifications in membrane before those in cartilage of both skull and vertebral column. The first differentiation to form the primordial cranium which we have observed is at Stage P, and it consists mainly of pro-cartilage. It can be resolved into two perfectly distinct portions, excluding the mandibular arch—an anterior common to the olfactory and the trabecular regions, a posterior involving the sphenoccipital and auditory regions [2]. Dealing with these individually, the anterior portion is seen to embrace the trabeculæ (Pl. III. figs. 1 & 2, *tr.*) and an ethmoidal constituent, consisting of an extensive basal plate with two pairs of outgrowths—an anterior or olfactory pair (*n.e.*) and a posterior pair—to be hereafter termed the *ethmosphenoidal plates* (*e.s.*), The trabeculæ (*tr.*), widely separated and enclosing a spacious pituitary foramen (*py.'*), are already hyaline, and pass gradually into the lateral edges of the basal ethmoid. The

[1] Gaupp, E.: Verhandlg. anat. Gesellsch. Sammlg. v. (Anat. Anz. Bd. iii., Suppl.) pp. 114, 120 (1891), also ibid. Sammlg. xii. (Anat. Anz. Bd. xiv., Suppl.) pp. 157–163 (1898), and Ber. naturf. Gesellsch. Freiburg i. B. Bd. x. pp. 302–316 (1898).

[2] Left uncoloured in our illustrations. Concerning the embryo which furnished the sections for figs. 1 to 3, Pl. III., it is regrettable that before investigating it we had handed it on to another, who, in decapitating it for other use, had cut through the auditory region. We found, however, on examination of slightly younger specimens, evidence sufficient for the extension of the differentiation into pro-cartilage into the regions included in the dotted lines in the figs.

posterior portion, at this stage disposed at right angles to the anterior (its anterior extremity being alone visible from above, as in fig. 2), is seen to similarly consist of a basal or parachordal plate (*par.*) also bearing two pairs of outgrowths, viz. an anterior (*o.s.*), to be hereafter termed the *otosphenoidal plate*, and a posterior, the auditory capsule (*c.au.*). This posterior portion is hyaline only at the anterior and lateral borders of the parachordal plate, the anterior chondrification extending into each of the otosphenoidal tracts. The intracranial notochord, enclosed within the basal parachordal plate, terminates anteriorly in a minute freely-exposed apex (*nc.*, fig. 2), and, as already pointed out by Dendy for Stage N (99 [a]. p. 75), it takes a sinuous course.

Dismissing for the present the sensory capsules, which at this stage are simple and cup-shaped, it becomes necessary for comparison of later stages to deal fully with the ethmo- and oto-sphenoidal plates. The former (*es.*) are large and wing-like and bear no outgrowths. The latter are complex and wholly distinct from the trabeculæ. Each of these otosphenoidal plates is seen to be extending upwards and outwards, backwards and inwards, and directly forwards. Two apertures are enclosed by it—a lower (*f. iii.*), which transmits the third cranial nerve, and an upper (*f. iv.*), which transmits the fourth [1]. The processes to which it is giving rise (indicative of differentiation along definite lines) are five in number (*os.*[1] to *os.*[5], Pl. III. figs. 1, 2, 3).

Before passing on to a later stage, we wish to emphasize the simple rod-like condition and non-extension into the cranial wall of the trabeculæ, which, except for their connection with the procartilaginous basal ethmoid, are disposed serially with the mandibular arch (*pg.mk.*).

At Stage Q, despite the short advance in time upon P, remarkable progress is seen to have been made in the formation more particularly of the cranium, nearly all the definitive components of which are now recognizable. The trabeculæ have now fused posteriorly with the parachordal—not by their ends as might be supposed, but by their postero-internal borders,—and they appear to us now to give rise to the basipterygoid outgrowths (*bs.'*, Pl. III. fig. 6). An accompanying upward rotation of the parachordal (associated with cranial flexure) has brought about a consequent approximation of the otosphenoidal plates to the trabeculæ, with an accompanying fusion involving the first and fifth otosphenoidal processes. Of these, the latter, passing downwards, unites with the outer trabecular border, and thereby shuts off (*f.j.*, fig. 4) a jugular foramen; the former, uniting with the inner trabecular border, encloses a passage (*f.a.*) for the ophthalmic artery.

More significant than the foreging is the change in position undergone by the second and third otosphenoidal processes. Originally directed upwards, under the combined influence of rotation and growth, they are now directed forwards, and, by union with the posterior border of the sphenethmoidal plate, they have come to bridge longitudinally the membranous lateral cranial wall. As the result of this, two

[1] Gaupp (1898, Berichte, p. 8) describes these nerves in the Lacertilian as related to a common fenestra.

further fenestræ arise in the same vertical plane in front of those already described. Of these the upper or *lateral cranial fenestra* (*f.n.*, Pl. III. figs. 4, 6, 7) is wholly membranous, transmitting nothing, the lower (*f. ii.*) giving passage to the optic nerve. It will further be noted that with the establishment of this union between the ethmo- and otosphenoidal plates the parts most nearly related to the latter have become expanded and carried up by growth of the basi-ethmoidal plate, together with which they constitute a considerable cartilaginous interorbital septum.

The fourth otosphenoidal process, originally directed downwards (*os.*^{4}, fig. 1), now carried up, looks straight backwards (*cf.* figs. 5 & 8), but it has remained free.

On appreciation of these important processes, which have effected so marked a change in the configuration of the parts, it is evident that growth must be most rapid in the otic border of the otosphenoidal plate.

The chrondrocranium at this stage, viewed from beneath, reveals changes which, though less dominant than those described above, are in themselves remarkable. Massive indeed have the basis cranii and auditory capsules become, under the accelerated growth associated with the straightening of the basi-cranial axis and the marked lateral expansion of the post-pituitary floor (*cf.* figs. 6 & 7). The occipital region has now become conspicuous, by the upgrowth on either side (*e.o.*, Pl. III. figs. 6 & 7) of a considerable cartilaginous lobe lying free of the auditory capsule, between which and it there lies the huge interspace for the 9th, 10th, and 11th cranial nerves (figs. 6 & 7, *f. ix.* to *xi.*).

Anteriorly to the trabeculæ the basal ethmoidal plate (*cf.* fig. 6), vertically extended as has been seen, has undergone a forward growth—as is proved by the fact that its length is now as great as that of the trabeculæ themselves, and it has also undergone a downward rotation, very marked as viewed from the side (Pl. III. fig. 4).

The pituitary foramen at this stage (*py.'*, Pl. III. figs. 6 & 7), compared with that of Stage P, as represented in the accompanying figs. (*cf.* fig. 2), would seem to have undergone considerable reduction with advancing growth. When, however, it is remembered that the figure of Stage P (fig. 2) is magnified 13 times, that of Q (figs. 6 & 7) but 8, it will be evident that under the growth-changes going on the trabecular tracts which more directly bound the foramen have been well-nigh stationary, and that such reduction of the foramen as has taken place would appear to be rather due to the mode of union between the trabeculæ and parachordal cartilages than to actual cartilaginous invasion.

Finally, as to the sense-capsules—now both chondrified. With the olfactory capsule complication has set in. Its capsular portion (*nc.*) has entered into a union with the anterior border of the ethmosphenoidal plate, giving off dorsally a short *supranasal process* (*nc.'*, fig. 4) connected with the plate by an *ethmonasal bar* (*e.b.*) lying within the outer border of the olfactory nerve foramen. At its anterior extremity it gives off a *prænasal process* (*nc.''*, fig. 4), which embraces the anterior wall of the nasal sac.

Somewhat similarly related to the postero-external wall of the sac is a large quadrangular cartilage, the *extranasal* (*ex.*), and from this four processes arise. The two anterior of these (*ex.* 1 & 2) are united to the ethmoidal bar so as to enclose a fenestra (*n.f.'*). The two posterior are free, and the third (*ex.* 3), together with the posterior half of the parent cartilage, disposed at a sharp angle to the external half of this, contributes to the support of the anterior orbital wall, bounding ventrally the ethmoidal foramen (*f.e.*), which transmits the ophthalmic branch of the fifth nerve [1].

In addition to these complex nasal supports, there is present at this stage in the nasal floor a sheet of procartilage which, in order to complete our terminology, we name the *subnasal*. This, to which we shall return, is wholly independent in origin, and by analogy to the extranasal we suspect that this may also arise independently.

The only remaining changes in the chondrocranium are mainly of the nature of advancing completion of the parts now described. No new elements are added after Stage Q. These perfecting processes, as they may aptly be termed, are most conspicuous at Stages R and T, which may accordingly be dealt with independently.

Stage R.—A very striking feature of this, as compared with the earlier stages, is the straightening out of the ethmosphenoidal region, which at Q was downwardly rotated (*cf.* Pl. III. figs. 4 & 8). This straightening process affects most conspicuously the median parts (internasal septum), which now appear as if withdrawn under cover of the extranasal cartilage (*ex.*, fig. 8).

Equally striking are changes involving the antorbital and otoccipital regions. That taking place in the former is of the nature of extension most markedly dorsalwards of the interorbital septum (*s.i.*), by continuation of the process of elevation of the basal ethmoid already alluded to (*antea*, p. 39). Under the combined influences at work, growth has become more rapid with the ethmosphenoidal than with the otosphenoidal plate; and ready proof of this lies in the now upward direction of the third otosphenoidal process (*os.*^{3}, fig. 1), which at Stage Q (*os.*^{3}, fig. 4) was arched and reached the highest point. Of the fenestræ described at Q (which in life are closed by membrane, except where they transmit nerves) only one has undergone change, viz. that transmitting the fourth cranial nerve (*f.* 4, fig. 8). This is now complicated, having become continuous with the fenestræ transmitting the third cranial nerve, the jugular vein, and ophthalmic artery—all four being now closed by one continuous membranous sheet. It is clear, on comparison with Stage Q, that the cartilaginous bridges which originally separated these fenestræ (*i. e.*, the fifth otosphenoidal cartilage and its near neighbours) have been absorbed.

As an accompaniment of these changes, the small cartilaginous bar bounding at

[1] *Cf.* Osawa, 98[a], p. 504.

Stage Q the front of the foramen for the fourth nerve has become much elongated and brought into line with the second otosphenoidal process, so as to give the appearance of a continuous bar. That this is not the case, however, is proved by the fact that the second otosphenoidal process in reality is now represented by the insignificant tract (fig. 8, *os.*^{2}) lying between the ventral extremity of the cranial fenestra (*f.n.*) above and the dorsal extremity of the optic fenestra (*f.''*) below. Its apparent forward continuation at this stage is due to the appearance in the cartilaginous interorbital septum of yet another fenestra (*f.i.*, Pl. III. fig. 8), which is of necessity median. Like the lateral cranial fenestra (*f.n.*), it is wholly membranous, and it alone merits the term *interorbital fenestra*.

Turning to the occipital region, the foramen magnum is now seen to be completely surrounded in cartilage, as the result of union between the upper ends of the occipital cartilaginous lobes and the posterior walls of the auditory capsules, resulting (*cf.* Pl. III. fig. 9, *e.o.*) in the enclosure of the afore-mentioned interspace transmitting the cranial nerves ix. to xi. above, and its conversion into a foramen. With these changes another, probably correlated with the afore-mentioned upheaval of the ethmosphenoidal plates, is recognizable, viz. the appearance in the postero-dorsal cranial roof of a spatulate cartilage (*so.'*, Pl. III. figs. 8 & 11), which in its general relationships recalls that figured and described by Parker [1] in *Lacerta* and *Zootoca* as "supra-occipital." This is seen to arise posteriorly from a massive tract of cartilage overlying the foramen magnum, which appears to us more extensively derived by the overarching of the auditory capsules than of the occipital lobes. When the chondrocranium is viewed from the side, at this stage, this "occipital" cartilage is seen to be arched, and to follow, with the antero-dorsal border of the expanded ethmosphenoidal plate, the arc of the circle described by the top of the head, which at the earlier stage was followed by the third otosphenoidal process (*os.*^{3}, Pl. III. fig. 5). In this respect, the two may be said to have been correlatively modified in accommodation to the roofing-in of the brain, now possible under the diminution in relative rapidity of the growth of the central nervous system.

An interesting detail at this stage is the presence in the basi-occipital region of a minute depression, involving the lower border of the foramen magnum. Conversely, the ventro-lateral border is on either side rounded and convex, the whole giving to the chondrocranium, especially when viewed from above (Pl. III. fig. 11) or from beneath (fig. 12), the appearance (as has been pointed out by Gaupp [2] for the embryo lacertilian) of being doubly condylar.

In the nasal region the extranasal cartilage (*ex.*, Pl. III. fig. 8) has increased in size, but it has undergone no conspicuous change, except for the elongation of the

[1] Parker, W. K.: Phil. Trans, 1879, p. 595.

[2] Gaupp, A.: 1898, Berichte, p. 6.

fourth of its processes (*ex.*^{4}), which now lies in an interspace between the palatine and maxilla (*cf.* fig. X., *ex.*^{4})[1]. The subnasal sheet (*sb.*), now chondrified, wherefore it may be termed the *subnasal cartilage*, has entered into continuity by means of a delicate cartilaginous bar with the prænasal process (*nc.*$''$) of the primitive olfactory capsule, and by a less considerable bar with the extranasal cartilage (*ex.*, fig. 8). It extends inwards, partly underlying the vomers, and effects (as indicated in fig. 12, *s.b.*) an infolding of the outer lip of the posterior nares.

Stage T.—At this stage the characters of the definitive chondrocranium are all present, and, owing to the increase in size, we found it unnecessary in dealing with it to resort to microscopic sections and reconstruction. Fig. 10, Pl. IV., delineates from the left side this chondrocranium, divested of all dermal elements except the parasphenoid (*ps.*), now co-ossified with the basisphenoid (*bs.*). The most conspicuous changes to be observed are two, (i.) the backward extension of the fourth otosphenoidal process (*os.*^{4}) and its fusion with the auditory capsule at the base of the supraoccipital bridge, (ii.) the elongation of the ethmo-nasal region, which is a main factor in the final realization of the adult proportions and shape of the skull. As the result of the fusion above-named, the lateral chondrocranial wall is now in a condition of uninterrupted continuity dorsally with the olfactory and auditory capsules, and the passage transmitting the fifth cranial nerve now becomes a perforated fenestra. In proportion, size, and shape, the fenestræ have undergone a considerable amount of change, mainly associated with the cartilaginous extension of the interorbital septum (*s.i.*). By the extension of the lateral cranial wall, the process of closing in of the roof has advanced, but there is no change of importance as compared with the preceding stage.

The nasal capsule has become modified by the fenestration (*n.f.*$'''$) of the extranasal cartilage.

The cartilage-bones (which appear at Stage R, but, owing to their then feeble condition, are not represented in our accompanying figures of the models at that, figs. 9 & 12, Pl. III.) are seen assuming shape at S (figs. 4, 5, 6, & 7), but at T they are in the condition most favourable for description. They are 9 in all—3 median and 3 paired—and with the exception of the basisphenoid all are otoccipital.

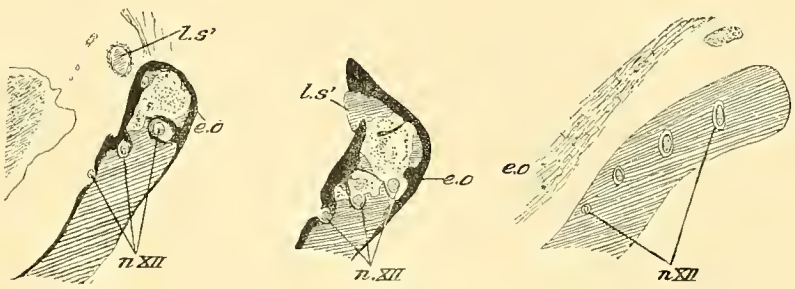
When the skull is examined from beneath (Pl. IV. fig. 6) the basisphenoid (*b.s.*) and basi-occipital (*b.o.*) are seen to arise within the anterior and posterior regions of the post-pituitary floor. The former extends laterally into the cartilaginous basipterygoid processes (*bs'.*)[2], which at Stage T terminate externally in dilated extremities, for articulation of the pterygoid bones; and it also extends forwardly into the trabecular

[1] This is presumably the "processus maxillarius posterior" of Gaupp, which he aptly compares with the "antorbital" or palatal bar of the Anura and Ranodon (1898, Berichte, p. 8).

[2] We have found traces in transverse section at Stages R–S of the paired ossification asserted by Baur (Zool. Anz. Bd. xii. p. 45) to hold good for the basisphenoid and stated by Parker to be present in the Lacertilia ('Morphology of Skull,' 1877, p. 216).

region, so as to enclose the pituitary foramen, now undergrown by the parasphenoid (*cf.* transverse section, Pl. IV. fig. 3). The basi-occipital (*b.o.*) arises from a single ossific centre. The exoccipitals arise as ossifications of the occipital lobes of the chondrocranium, and by extension reach the posterior boundary of the exit for the ninth to the eleventh cranial nerves. Osawa has recently described (98[a]. p. 494), with perfect accuracy, the adult condition of the nerve-foramina which result from this, and concerning the hypoglossal foramina he gives two as the number present. He also describes

Fig. 7. Fig. 8. Fig. 9.



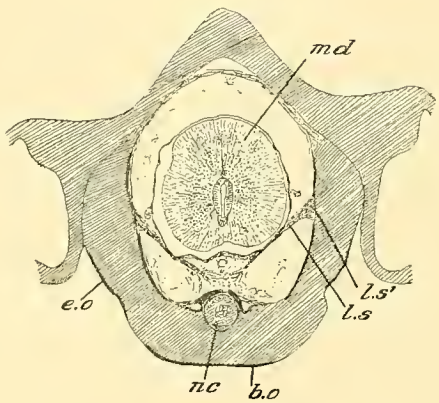


Fig. 10.

Figs. 7 to 10.—Sections through the occipital region of *Sphenodon* showing the hypoglossus nerve-foramina at different stages of development, and the sustentacular ligaments of the medulla. 7 and 8. Lateral longitudinal sections at Stage S, × 33. 9. Lateral longitudinal section at Stage Q, × 67. 10. Transverse section at Stage R, × 33.

b.o., basiocepital; *e.o.*, exoccipital; *l.s.*, sustentacular ligament; *l.s.'*, its exoccipital support; *md.*, medulla oblongata; *nc.*, notochord; *n. xii.*, hypoglossal nerve-roots and foramina.

two nerve-roots. Gaupp accords a third hypoglossal foramen to the embryo Lacertilian (Berichte, p. 5). Interesting this, in consideration of modern discovery concerning the truncal origin of the hypoglossal nerve-bearing region of the skull. Still more interesting when we record the fact that, whereas in Sphenodon, at Stage S, three hypoglossal foramina are present, with corresponding nerve-roots (*n. xii.*, text-figs. 7 and 8),

at Q (text-fig. 9) there are four foramina and five roots. It is certain that, during ontogeny, two roots at least disappear, and further investigation is necessary to render perfectly clear the detailed nature of those which remain [1].

We may most fittingly refer here to a series of ligamentous supports which, so far as we can ascertain, are new. We first detected them at Stage Q in the occipital region. At S each is very conspicuous, and with its fellow of the opposite side is closely applied to the under face of the medulla oblongata. It is strengthened at its bases by ingrowths of the occipital cartilage (*l.s.'*, text-figs. 7, 8, & 10), and in the floor of the neural canal it enters into a loose fibrous connection with the dura mater (*cf.* fig. 10). This remarkable structure is repeated segmentally throughout the trunk-region of the vertebral column, and we propose to term it the *sustentacular ligament.*

The supra-occipital calls for no special comment.

The opisthotic (*op.*, Pl. IV. fig. 9), which Siebenrock has proved [2], to be an independent element (the "paroccipital" of Owen), is at this stage remote from both the prootic and exoccipital, and the ossific centre of the former is now beginning to monopolize the feebly-developed cartilaginous parotic process (*p.p.*), which appeared at Stage Q and is still short. The prootic ("otosphenoid," auct.) (*pro.*, figs. 8 & 10) is a simple bone, and its processus anterius inferior, so characteristic of the adult [3], has not yet appeared, nor has ossification yet encroached upon the processus anterius superior, which, still hyaline, forms (*cf.* fig. 8, *c'.*) not only at this, but at Stages R and S, a formidable projection.

The Mandibular Arch.—This is first differentiated at Stage P, in the form of a minutely procartilaginous mass having a body or quadrate portion (Pl. III. fig. 1, *q.*) bearing three outgrowths: an antero-dorsal or pterygoid (*p.g.'*), a postero-dorsal—the future epipterygoid (columella), *epg.*,—and an antero-ventral, much the stronger of the three, the Meckelian bar (*mk.*).

The main body or quadrate mass, at this stage somewhat squarish, is disposed parallel with the parachordal (*pc.*), and throughout the later stages, at which the rotation of the latter and the straightening out of the basis cranii already referred to are effected, it retains this relationship, *i. e.*, the absolutely distinctive characters of the whole arch are present in procartilage. Chondrification is seen to be setting in independently in its body and the Meckelian bar, and even at this early stage the latter is connected with its fellow symphysially by a thin procartilaginous tract. At Q advancing chondrification of the Meckel's cartilage invades the symphysial tract, and the whole cartilaginous lower jaw becomes for the time a single hyaline mass. It remains such until Stage T, when the definitive symphysis begins to appear.

[1] *Cf.* Peter on *Ichthyophis* (footnote, *infra* p. 70).

[2] Siebenrock, F.: 1893, p. 304, English Transl.

[3] *Cf.* Siebenrock, F.: Transl. cit. p. 307, & fig. 14, pl. 10. & Brühl, 'Zootomie aller Thier Kl.' pl. 149. fig. 5.

With advancing development, the chondrifying centre of the quadrate cartilage extends into the pterygoid and epipterygoid processes in common, and with this replacement there comes about the afore-mentioned rotation, under which the epipterygoid process, originally directed backwards and downwards, comes to be upwardly directed, the pterygoid bar being displaced accordingly. On the assumption of this rotation and its definitive position, the quadrate portion elongates and develops two processes—a dorsal or otic process (fig. 4, *q.'*), and a lower process, which appears correlatively with the segmentation off of Meckel's cartilage. Anteriorly its pterygoid portion turns suddenly outwards and expands (*cf.* espec. Pl. III. fig. 6, *pg.'*). Continuing to elongate, it comes at Stage R to overlie the pterygoid and the inner half of the os transversum, tapering to a point. Gaupp describes this cartilage in the Lacertilian as merely extending "in the direction of" the transversum. He points out (Berichte, p. 9) that did it continue forwards it would enter the maxillary region and that of the processus maxillarius posterior (our fourth extranasal process) of the nasal capsule, it would realize the condition occurring in Ranodon and the Anura. With this we fully agree; but we regard the extension over the transversum as indicative of the retention by Sphenodon of a more approximately batrachian condition than that thus far known for the Lacertilia.

In Sphenodon the study of the nerves and all possible relationships leaves no doubt that the epipterygoid process is the homologue of the processus ascendens of the batrachian quadrate cartilage, as recognized by Gaupp. He, however, seems to us somewhat in doubt [1] as to the actual occurrence in the Lacertilian embryo of a cartilaginous connection between the epipterygoid "Anlage" and the quadrate. In Sphenodon, so far from there being any doubt on this matter, not only are the epipterygoid and quadrate originally præformed in one continuous cartilaginous tract, but, from Stage R onwards, the portion of this which, after the establishment of these two bones, remains, begins to ossify by extension of the quadrate centre, to form the characteristic antero-dorsal quadrate lobe (Pl. IV. fig. 11), the presence of which accounts for the close relationship of the epipterygoid and the quadrate in the adult. The difference with the reduction of the jugal arch and the liberation and freedom of the quadrate associated in the Lacertilia is one in respect to which the gap between these and the Rhynchocephalia is immensely greater than between them and the Chelonia [2], to say nothing of the Crocodilia and other reptiles possessed of a fixed

[1] Gaupp, E., especially in his paper in Anat. Anz. Bd. vi. 1891, p. 107, and Berichte *cit.* 1898, pp. 9–11.

[2] We can only express astonishment, mixed with regret, at the gratuitous assumption by Osawa (98 °, p. 102), in seeking to explain away the Güntherian dictum concerning the relationships of the quadrate to the pterygoid, that the latter arises from two ossific centres, of which the hinder has in Sphenodon become co-ossified with the quadrate. There is no trace of any such posterior pterygoid bone actual or potential.

quadrate. And in this connection it may be remarked that if the detailed configuration of the cartilaginous upper jaw be a criterion of relationship, the fact that a near approach to the condition occurring in Sphenodon is that of the Cæcilian Ichthyophis glutinosa as recently described by Winslow [1] is of great interest, when it is remembered that these Apodal Batrachia, in the possession of dermal ossifications and other well-known characters, are the most approximately Stegocephalian of all living forms [2].

The Hyoid and Columella auris.—Our observations concerning the hyoid apart from its connection with the auditory apparatus are few. At the earliest stage we have examined (viz. P) it has already appeared in procartilage in the form it assumes in the adult, except for slight differences in general proportion, as is better seen at Stage Q (Pl. III. fig. 4). We have no evidence pointing to a compound origin of its basal portion such as that described by Gaupp [3] for the Amphibian, or of the complexity in structure of the order described by Siebenrock [4] for the Chelonia.

It is only as concerning the vexed question of the relationship between the columella auris and the anterior cornu of the hyoid that we need proceed to details. The nature of this in the adult has been so oft recapitulated that it will suffice to point out once more that, apart from theories based on alternative interpretations of the facts of adult anatomy and surmises necessary for their defence, the real question developmentally at issue is whether or not the hyoid cornu and the extrastapedial are secondarily united, and whether the object called by Huxley suprastapedial does or does not arise independently.

Huxley, in describing the parts of the adult, regarded [5] the whole columellar complex as hyoidean, and the extra- and suprastapedial processes as parts of its expanded outer extremity. Peters, and all subsequent investigators [6], on the contrary, with the exception of Versluys, who has recently argued [7] in favour of original continuity, have assumed that the connection between the extrastapedial and the hyoid cornu is secondary, while Peters more especially believed the suprastapedial to have been originally distinct. As great testimony to the extreme care with which Huxley worked at this problem, there stands the fact that he drew attention (*op. cit.* p. 398) to the presence, on the inner side of the foramen (*f.h.*, text-fig. 11, which for brevity's sake we associate with his name), of a fibrous differentiation included between the extra- and suprastapedial processes.

[1] Winslow, G. M.: Tuft's Coll. Stud. vol. i. no. 5, 1898, pl. iii. fig. 24.

[2] *Cf.* Boulenger, G. A.: P. Z. S. 1895, p. 402.

[3] Gaupp, E.: Morph. Arbeiten, Jena, Bd. iii. 1894, p. 399.

[4] Siebenrock, F.: Ann. naturhist. Hofmus. Wien, Bd. xiii. 1898, p. 424.

[5] Huxley, T. H.: P. Z. S. 1869, p. 391.

[6] Peters, W.: Monatsber. Akad. Wiss. Berlin, 1870, p. 15, and ibid. 1874, p. 40. *Cf.* also Baur, G.: Biol. Centralbl. Bd. vi. 1887, p. 655; Killian, G.: Jen. Zeitschr. Bd. xxiv. 1890, p. 649; Osawa, G.: 98 [a], p. 520.

[7] Versluys, Jan.: Zool. Jahrb. Anat. Abth. Bd. xii. 1899, p. 167.

Gadow alone among recent investigators has carefully examined a series of individuals, and he records further details. Chief among these is the discovery[1] that the Huxleyean foramen may be reduced to the size of a pin-hole or absent (*op. cit.* p. 467)—facts which point to the conclusion that its condition is indicative of variation in degree of extension of chondrification, especially when it is remembered that it transmits nothing.

Huxley described the head of the suprastapedial process (p. 397) as connected with the parotic cartilage of the skull. Gadow, on the other hand, records in one example a ligamentous attachment to this; he remarks of another that "it does not touch the cranium" (p. 468); and of a third he writes, the hyoid is continued "along the anterior and lower margin of the extra-columellar cartilage, upwards to the parotic corner, when it does not fuse with, although it directly touches, the cranial cartilage." Sufficient this to show that the suprastapedial is in its ultimate attachment variable.

With these facts in mind, we were especially attentive to the extrastapedial region, and concerning it the following:—Examined at Stage S, and onwards to those stages in which the adult condition is assumed, lateral longitudinal sections through the quadrate (Pl. V. figs. 13 & 14) show that bone to be unossified dorsally. It is seen to be overlain by the squamosal (*sq.*), and when successive sections are followed outwards the extrastapedial process (*e.c.*) is seen in the inner series to pass (Pl. IV. fig. 13) into the suprastapedial (*s.st.*). As the sections become external the suprastapedial is seen to approach the head of the quadrate and eventually to fuse with it, as in fig. 14 (*s.st.*), which passes through the Huxleyean foramen. Sections more superficial, as regarding the continuity of the parts, combine the appearance of these two figures. Examination of the whole series and dissection alike reveals (*cf.* Pl. IV. figs. 7 & 9) an absence of cartilaginous connection with the skull; and in the denial of this we are in agreement with Gadow.

The foregoing observations would at first sight appear contradictory to Huxley's. Examination of his fig. 4, however, reveals an error, in the fact that he has indicated as the exoccipital the parotic process of the opisthotic, as is proved by his delineation of its articular extremity. Allowing for this correction, his "parotic cartilage" can only represent the articular head of the quadrate; and, if so, his description amounts to that of a union between the suprastapedial and the quadrate, such as we have described and have observed not only at Stage S but at T. And, as a consequence of this, it follows that cartilaginous continuity between the suprastapedial and the skull does not exist, and that the quadratic union applies to the adult as well as to the young. Resorting to the earlier stages, with a view of ascertaining whether this union is or is not primary, we find in sections at Stage R that it does not

[1] Gadow, H.: Phil. Trans. 179 B, 1889, p. 468.

exist (*cf.* Pl. V. fig. 12), the quadrate head (*q'.*) and suprastapedial process (*s.st.*) being distinct though closely approximate. Passing to Stage Q (figs. 10 & 11), the distance between the two is seen to be much greater, the nearest approximation being that of fig. 11.

Turning now to the suprastapedial process, and the fibrous interval of Huxley. The former arises at Stage Q as a simple upgrowth, seen in section at fig. 10, Pl. V., *s.st.* When Stage R is reached, this is seen to be still elongating (text-fig. 11, *s.st.*) and to have given rise at the middle of its inner border to a recurrent process (*s.st.'*), which, passing downwards and inwards, becomes apposed to the columella auris (*st.*), to which it is tied by a series of fibres, which pass obliquely between the two. Between its recurved lower extremity and the columella a non-hyaline tract is present (*, fig. 12)

Fig. 11.

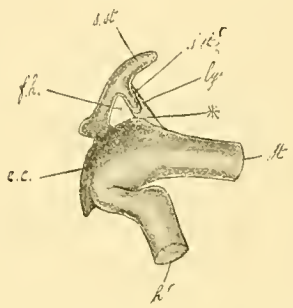


Fig. 12.

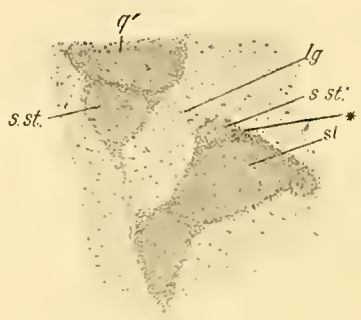


Fig. 11. Drawing from a reconstructional model, showing the detailed characters of the columellar head of *Sphenodon* and its derivative processes at Stage R, × 30. Fig. 12. Microscopic section through the same, parallel to the columellar axis, × 75.

e.c., extrastapedial; *f.h.*, foramen of Huxley; *h'.*, anterior cornu of hyoid; *lg.*, ligamentous fibres; *q'.*, upper end of quadrate; *s.st.*, suprastapedial: *s.st'.*, recurrent process of the same.

which we conclude is that described by Huxley. It remains only to add that as the process is absent at Stage Q it is of secondary occurrence.

As to the continuity between the hyoid cornu and the outer head of the columella (extrastapedial process), we have evidence that for the earliest stages of differentiation (P especially), when all the parts concerned are in the procartilaginous state, it is complete; but a very interesting detail arises—viz., that in some of a series of thick sections which we possess there can be observed (Pl. V. fig. 5, *) a very feeble suggestion of jointing, so feeble that it would be likely to be overlooked by anyone not familiar with the sections. This, however, cannot be regarded as evidence of original discontinuity between the columella and the hyoid cornu! It is seen to be but a passing phase, indicative of either a probable ancestral or an incipient "jointing" such as takes place elsewhere along the cornu (**); and, as compared with a later

differentiation occurring at the base of the extrastapedial (Pl. V. fig. 12 *b*), the primary independence of which has never been suggested [1], it is insignificant indeed.

Holding the foregoing facts proof sufficient that the columella, extra- and supra-stapedial are but the products of specialization of the upper extremity of the hyoid arch, with which they are at all stages continuous, we have in conclusion to direct attention to some puzzling procartilaginous tracts, of which we have been unable to detect a counterpart at a later stage. They are of the nature of two pairs of rounded masses (one of which is represented in Pl. V. fig. 1,†) disposed serially between the roof of the pharynx and the auditory capsule, ventrad of the fenestra ovalis region, and we are unable to hazard a guess at their significance.

Concerning the chondrification of the columella and the related anterior cornu of the hyoid, we find at Stage Q, when the procartilaginous tracts above described become hyaline, that all traces of the "jointing" disappear. Examination of figs. 6 to 9 (Pl. V.) shows this conclusively, and also that the hyoid cornu (*h.'*) passes continuously into the extrastapedial (*ec.*), and through that into the columella (*st.*). The inner head of the latter, seen at the procartilaginous stage (Pl. V. figs. 3 & 4, *st.*) to merge into the feebly differentiated mass (*c.au.*) giving rise to the auditory capsule, at the period of chondrification is seen to be structurally continuous with that now hyaline, and in section (Pl. V. fig. 6, *st.*) delimitable only by a close approximation of its peripheral cells. Later, it becomes free, and attached to the rim of the fenestra ovalis by membrane, in the customary fashion (*cf.* Pl. V. fig. 12, *st.*). Its rod-like portion commences to ossify superficially, in the manner of the parts of the vertebral column and the otoccipital bones.

The Trabeculæ.—One very conspicuous feature of the afore-described stages in the development of the chondrocranium is the non-extension or incorporation of the trabeculæ into the lateral cranial wall. As pointed out (*anteà*, p. 38), these remain passive during the development of this.

Examination of the adult chondrocranium of Sphenodon, apart from a knowledge of its development, might well arouse the supposition that its fenestræ are due to absorption of an originally continuous wall, of the cartilaginous fish type. One of the most certain and fascinating of our results is the discovery that the cartilaginous cranial bars are all due to continuous-growth processes, that the correlated fenestræ are in no way due to absorption, and that the trabeculæ play no part in the formation of the lateral cranial wall. From first to last these are simple rods, lost by union

[1] Kingsley, the latest worker who has dared to deal with the subject of the general morphology of the auditory ossicles (with which we are not concerned), expresses his conviction (Tufts Coll. Studies, No. 6, 1900, pp. 215–216) that the Lacertilian hyoid and columella are originally continuous in the embryo. He claims for the "extra columella" an independent origin, but since he uses the term in an unconventional sense and his figure (which does not bear out his description) leaves us in doubt whether his "extra columella" may not represent the supra-stapedial process, we feel justified in the above statement.

anteriorly with the basal ethmoid, united by their postero-internal extremities with the parachordal; and, what is more, they are serially disposed at all stages with the visceral skeletal arches.

Recent investigation by the reconstruction method has led to the conclusion that the developmental processes occurring in the skull of Man himself are not easily reconcilable with those generally believed to be passed through by even that of certain other mammals [1].

As is well known, Salensky in 1878 described [2] in the embryo Sturgeon a distinct cartilaginous centre for the lateral cranial wall; and Stöhr, in 1880, discovering that the parachordal of Triton [3] appears in two pieces, in 1882 showed [4] the basal portion of the chondrocranium of Rana to be complex, if not actually composed of three pairs of distinct elements—trabeculæ, "mesotic cartilages," and "occipital plates" (parachordals). Miss Platt has later described in Necturus [5] the dorsal part of the "crista trabeculæ" as paired, and instituted, on consultation with Sewertzoff, a comparison with the alisphenoidal cartilage originally described by him in Acanthias in 97 [6]. While Peter, in the same year as Miss Platt, recorded the formation in Ichthyophis [7] of so-called "dorsal trabeculæ." Most important of all, however, is the full monograph of Sewertzoff, which has appeared during the progress of our work, in which [8], bringing the whole subject to a focus, he shows that in the Elasmobranch Acanthias the trabeculæ take an insignificant share in the formation of the lateral cranial wall, and that this is mainly formed on either side from the above-mentioned distinct cartilages (termed by him the alisphenoidal), the pair of which, uniting with the trabeculæ, contribute what he has termed the prochordal portion of the resulting chondrocranium. In his memoir he meets the challenge that if this cartilage be of the importance he claims, it should be more generally forthcoming, by showing reason for its being present in Pristiurus, that W. K. Parker had seen it in the Salmon [9], and that other observers, and more particularly Miss Platt and Peter referred to above, had probably done so in other chordate forms. In view of this and of the similarity in posterior extension of the trabeculæ along the parachordal in Acanthias and Sphenodon, and of the relationships of the latter to our otosphenoidal plate (Pl. III. fig. 1), we consider that this may perhaps represent Sewertzoff's alisphenoidal cartilage [10].

[1] Levi, G.: Archiv mikr. Anat. Bd. lv. 1900, p. 407.

[2] Salensky, W.: Zool. Anz. Bd. i. 1878, p. 289.

[3] Stöhr, Ph.: Zeitschr. wiss. Zool. Bd. xxxiii. 1880, p. 477.

[4] Stöhr, Ph.: Ibid. Bd. xxxvi. 1882, p. 91.

[5] Platt, Miss Julia: Morph. Jahrb. Bd. xxv. 1897, p. 377.

[6] Sewertzoff, A.: Anat. Anz. Bd. xiii. 1897, p. 413.

[7] Peter, K.: Morph. Jahrb. Bd. xxv. 1898, p. 555.

[8] Sewertzoff, A.: Küpffer Festschrift, Jena, 1899, p. 281.

[9] Parker, W. K.: Phil. Trans. 1883, p. 129, pl. v.

[10] During the passage of this Memoir through the press, Sewertzoff has announced details concerning the development of the skull in the Gecko (*Ascalabotes fascicularis*) which fully supports this conclusion (*cf.* Anat. Anz. Bot. xviii. p. 36, 1900).

Far reaching as is his discovery, and interesting as are its bearings on our own work, we venture to think that the most rational interpretation to be put upon the behaviour of the trabeculæ in Sphenodon is that of Huxley, originally put forward in his Hunterian Lectures in 1864, that they represent a pair of præ-oral visceral arches. Huxley reiterated this conclusion in 1874, in his suggestive note on Amphioxus [1], and von Küpffer gave it consideration and support in 1893 [2], in his discovery of a pair of præ-oral visceral diverticula in the embryo Sturgeon. Further consideration of this very important topic is beyond the possibility of this memoir, but we hail with delight the discovery, as our work was nearing its termination, by von Davidoff, of the existence of this very pair of diverticula in the Lizards Platydactylus and Lacerta.

Cranio-facial Membrane-Bones.

The anatomy of these has been so fully dealt with by various authors, and most recently by Osawa (98[a]. p. 497), that we have little to add to their descriptions. Developmentally, however, some interesting considerations arise. At Stage Q, the earliest at which we have been able to observe membrane-bones, the vomers, palatines, pterygoids, maxillæ, postorbitals, squamosals, angularia, supra-angularia, and dentaries are all present (Pl. III. fig. 5) and remote from each other. By the time that R is reached, all the membrane-bones present in the adult are represented (*cf.* Pl. III. figs. 10–12). Looking at the skull from the side, this does not at first sight appear so, but when examined fully it is found that while the frontals are approximated in the middle line, the parietals are widely divaricated and small and of a remarkable angulated type. Examination of the skull at this stage shows that the frontal and postfrontal, the præfrontal, maxilla, jugal, and postorbital are all in close relationship, first active development having apparently involved those elements which are circumorbital—a fact which immediately impresses itself on the mind when, at this stage, the skull is viewed either from above (fig. 11) or the side (fig. 10). And one is led to speculate how far this may not be indicative of a first protection of the eye, when it is remembered that the palæontological record proves the circumorbital

[1] Huxley, T. H.: Proc. Royal Soc. vol. xxiii. 1874, p. 131.

There is evidence among Huxley's unpublished notes that in the early 80's he was returning to this conception and to work upon the skull. He was bringing to bear upon it the discovery in the Elasmobranchs of a fourth branch of the trigeminal nerve, to have been termed the *palato-nasal* or *hyporhinal*. This term was intended to express the fact that, in relation to the trabeculæ, this branch of the fifth cranial nerve, together with the ophthalmic (for which he had already introduced the correlative term *orbito-nasal*, in his article "Amphibia," Encyclop. Brit., Vol. i. Edit. 9, p. 767), repeats the condition of the other cranial nerves in relation to their visceral arches and clefts, and thereby presupposes the existence of a præ-oral cleft. And, further, he was building up an argument on this basis to show that in these facts there lies the explanation of the mode and point of termination anteriorly of the notochord.—G. B. H.

[2] Küpffer, C. von: Stud. d. vergl. Entwick. Kopfes d. Kranioten, Hft. i. *Acipenser*: München, 1893, p. 89.

region to have been the first seat in order of time of the development of dermal plates [1].

Passing to the palate, it is seen that at this stage approximation is most marked in front, for while the vomers have met in the middle line, the pterygoids are widely divaricated behind. A noticeable feature is the fact that the palatines, which support the orbital floor, have apparently shared in the afore-mentioned rapidity of growth. From this stage onwards, the salient feature in progressive development is the closing in towards the middle line of the bones of both the cranial roof and palate, rendered possible by the fact that the most rapid phases in the growth of the brain have now passed. Comparison of Pl. III. figs. 11 & 12, and Pl. IV. figs. 5, 6, and 8, will render clear the changes undergone in the individual bones during the process, which it is not necessary to describe in words.

It is at the stage (R) that the parasphenoid first appears, in the form (Pl. III. fig. 12, *p.s.*; in section in Pl. IV. fig. 1) of a minute bony element which would most certainly be lost to sight in ordinary dissection, lying freely beneath the antero-median border of the post-pituitary plate. With advancing development it assumes an arrow-head shape and a more intimate relationship with the basis cranii, fusing by its broad posterior extremity at Stage S with the basisphenoids, and closing the pituitary foramen as it does so by extension anteriorly (Pl. IV. fig. 3).

We have already drawn attention (*anteà*, p. 2) to the interest attaching to this bone. It was overlooked by Günther, Brühl, and others, and its discovery was first claimed by Fritsch, who believed he had observed it as an independent element [2]. Baur immediately challenged the alleged independence [3], and gave an accurate account of its limitations in a young individual. Fritsch compared the supposed parasphenoid with that of Hyloplesion, and comparison of his figure of this with that given by Credner (*op. cit.* p. 513) of the presumed co-ossified basi- and præsphenoids of Palæohatteria at once arouses suspicion by the close similarity in shape of the two; while further complication arises from the fact that Baur, commenting on Credner's discovery, regards [4] his basi-præsphenoid as a parasphenoid alone. Fritsch for Sphenodon, and Credner for Palæohatteria, were dealing with the compound basi- and parasphenoid, and were therefore in error. Baur was right only in his delimitation of the parasphenoid of Sphenodon.

The pterygoids, as already remarked, are developed widely apart, apposition in the middle line commencing anteriorly at Stage R, at which (Pl. III. fig. 12, *pg.*) they already reach the vomers—*i. e.*, their forward extension is thus recognizable as soon as

[1] *Cf.* Newberry, J. S.: Monogr. U.S. Geol. Survey, vol. xvi. 1889, p. 103, pl. xliv.; and Jæckel, O.: Sitzb. Ges. naturf. Fr. 1892, p. 90.

[2] Fritsch, A.: Fauna d. Gaskohle d. Permform. d. Böhmen, Bd. ii. 1889, p. 58.

[3] Baur, G.: Zoolog. Anzeiger, Bd. xii. 1889, p. 45.

[4] Baur, G.: Amer. Journ. Sci. 1889, p. 311.

the bones assume a mutual relationship, and is not brought about by ontogenetic growth. At Stage R (Pl. III. fig. 12) it will be observed that the anterior edge of the palatine (*pa.*) is transverse and that the vomers (*vo.*) lie wholly in front of them; whereas at Stage S (Pl. IV. fig. 6) the palatine border is angulated and the vomers are correspondingly modified. Proof that this change has arisen by backward elongation of the vomers, lies in the study of the relationships to the posterior nares, and it therefore follows that in the all-characteristic vomero-pterygoid apposition the vomer has played a part. Boulenger, one of the advocates of the Rhynchocephalian affinities of the Chelonia, has called special attention [1] to a similar apposition in this order; but concerning it the process is the reverse of that of the adult Rhynchocephalian, it being the vomer which for the most part reaches back to the pterygoid. Judged by the foregoing ontogenetic changes undergone by the developing Sphenodon, this feature, instead of presenting, as might appear, a difficulty in the way of the acceptation of the said affinity, strengthens it, since both bones are in both groups of animals involved in the apposition, though in an inverse degree.

In Ichthyosaurus the vomers extend back divaricatingly behind the nares, and the pterygoids, inserting themselves between them, extend forwards between the nares [2]. Taking the Stage R of Sphenodon as the starting point, the Ichthyosaur might well represent one extreme of modification, the Chelonian, through the adult Sphenodon, an opposite one; and in consideration of accepted views of the Chelonian affinities of the Plesiosauria [3], it is interesting indeed to find that in these they are the vomers which longitudinally extend [4].

The interest in the pterygoid of Sphenodon does not stop here, for, on examining its basicranial articulation we have found a synovial joint to be present and an independent interarticular cartilage (Pl. 4, figs. 1 & 3, *m.p.*), which flanks the inner face of the pterygoid and has an essential similarity to the meniscus mandibuli. We therefore propose to term it the *meniscus pterygoideus* [5].

Cognate to the study of the pterygoid is the presence of a process of the squamosal hitherto unrecognized, which (Pl. IV. fig. 11, *sq.'*) extends downwards and forwards between the quadrate and pterygoid, and, together with a process arising from the posterior border of the squamosal (*sq.''*, Pl. IV. fig. 9 and Pl. V. fig. 13), embraces the expanded otic head of the quadrate. Both are present in the adult, the hinder process being the less conspicuous of the two.

[1] Boulenger, G. A.: Brit. Mus. Catal. *cit.* p. 17.

[2] *Cf.* Baur, G.: Anat. Anz. Bd. x. 1895, p. 458, fig. 1.

[3] *Cf.* Andrews, C. W.: Quart. Journ. Geol. Soc. vol. lii. 1896, p. 251, fig. 2.

[4] *Cf.* Andrews, C. W.: Geol. Mag. (iv.) vol. iii. 1896, p. 4, and Ann. & Mag. Nat. Hist. (6) vol. xv. 1896, p. 345.

[5] Parker has undoubtedly seen and figured this in Zootoca (Phil. Trans. 1879, p. 612, & pl. 45. fig. 4), but his descriptive paragraph (§ 7) can hardly be said to adequately describe it.

The "Squamosal."—This bone has been most fully described by Baur, who [1] has accurately dealt with its relationships to the parietal, postorbital, jugal, quadrato-jugal, quadrate, and paroccipital process. It is unnecessary here to recapitulate the details of this association, which our figures render sufficiently clear, except to remark that we have extended the relationship to the pterygoid.

In the progress of investigation into the comparative osteology of the fossil reptiles, the varying conditions of the squamosal and supratemporal, one or both of which may be present, have become the subject of much consideration. The presence of the two has been regarded as a lowly characteristic, if only by way of analogy to the Stegocephalia. Cope and Baur are conspicuous among those who have utilized these bones in the determination and discussion of affinity, and nothing short of a deplorable confusion has arisen from their inconsistency in the usage of terms [2], and the fact that while one of them arrived at an inversion of the order adopted by certain contemporary writers, he finally complicated matters [3] by needlessly reviving for the reptilian squamosal Owen's term "prosquamosal." A final agreement was never arrived at, and the question therefore arises as to which of the two bones is for the future to be regarded as the supra-temporal.

As a general rule these bones lie side by side in the same transverse plane. The term supra-temporal was applied by Bakker to the inner one [4], in dealing with the fish skull. Cuvier denoted the presumably homologous bone in reptiles the "mastoid" [5]; and Owen, retaining this term, applied [6] to the outer of the two (Cuvier's "temporal") the term squamosal. To be consistent, therefore, on the assumption that the inner of the two bones, having similar relationships in fishes and reptiles, is homologous, convenience and precision are met by terming the inner the supra-temporal, the outer the squamosal. And it is in this sense that we use these words [7].

Our knowledge of the palæontological history of the Rhynchocephalia has during recent years been materially advanced by the description by Lortet of remains from the Jurassic of France. In his memoir already cited (*antea*, p. 3) he drew attention in Saphæosaurus (Sauranodon) to a "parieto-squamosal" complex, in respect to which

[1] Baur, G.: Anat. Anz. Bd. x. 1895, p. 321.

[2] *Cf.* Baur, G.: Anat. Anz. Bd. i. 1886, p. 349, and Bd. ii. 1887, p. 657! and, as an awful example, the series of notes embodying the dispute between him and Cope in Amer. Nat. vols. xxix. & xxx.

[3] Baur, G.: Anat. Anz. Bd. x. 1895, p. 320.

[4] In Cuvier and Valenciennes, Hist. Nat. des Poissons, t. i. 1828, p. 338.

[5] Cuvier, F.; Ossemens Fossiles, t. x. 1836, p. 14.

[6] Owen, R.: Catal. Osteolog. Series R. Coll. Surgeons, vol. i. 1853 (table), p. xxxviii.

[7] Concerning the afore-mentioned confusion, Fraas for example, in his revisionary memoirs on the Ichthyosauria and Stegocephalia, following in respect to the latter the lead of Huxley, Miall, Fritsch, and Credner, refers to the inner bone as the squamosal, the outer as the supra-temporal. Zittel adopts the Huxleyean order for the Reptilia and Stegocephalia, with confusion arising out of the interpretation of the latter in the Lacertilia as the quadrato-jugal. Brühl is still more glaringly inconsistent and contradictory; while even

Boulenger first showed him [1] to be probably in error. Baur, accepting Boulenger's correction, has sought to show [2] that the bones regarded by him as the supra-temporal and squamosal lie within the area of the "squamosal" of Sphenodon, and that that bone is therefore compound. Shuffling the terms, he regarded the body of the latter with its laterally visible processes as a "prosquamosal" ("squamosal" *auct.*) and its posterior ascending process as the squamosal ("supra-temporal" *auct.*).

Seeking for evidence in snpport of this in the Tuatara, Baur admits that none was forthcoming in a skull of 25 mm. in length (*op. cit.* p. 321). Not only have we failed in all attempts to detect any such separation, but also to observe at any period traces of a second element. While we fully admit that this so-called "squamosal" of Sphenodon combines the structural relationships of the supra-temporal and squamosal as originally defined, failing the discovery of any trace of its supposed double nature, we are disposed, on consideration of the behaviour and all detailed relationships of the supra-temporal in the Lacertilia, to regard it as a squamosal, and to interpret its ascending limb, which meets the parotic process of the parietal, as secondarily acquired. The alternative would be the introduction of a new term, in which neither "squamosal" nor "temporal" were compounded, but we have no wish to render confusion more confounded. The future can only settle the question, and we are content to leave it to that.

The Quadrato-jugal.—This bone, as is well known, was first recognized in Sphenodon by Dollo [3], and later more fully described by Baur [4]. We have nothing to add to their descriptive account of it. Its most characteristic feature is its enclosure with the quadrate (*qu.* & *q.j.*, Pl. IV. figs. 7 & 9) of a conspicuous foramen. Osawa, the latest writer upon it, terms it (98[a]. pp. 499 & 520) the "tympanic," presumably on account of his inability to regard the mammalian tympanic as the homologue of the quadrate; and associated with the study of this bone there is a matter of no little importance, if, as we believe, the tendency of our time is in error.

Baur, in 1889, argued [5] against the generally accepted belief that the single

---

Smith Woodward is not uniform in his terminology. Boulenger, on the other hand, is so, and, like ourselves, he retains the terms for the bones to which they were originally applied—*i. e.* for him, in both fishes and reptiles, the inner is the supra-temporal, the outer the squamosal. Difficulty admittedly arises when but one bone is present, and there is no doubt that in many such cases the problem can only be solved developmentally; but, on comparison of those lizards in which both bones are present, we believe him to be right in regarding the bone which alone suspends the quadrate in the Ophidia (Brit. Mus. Cat. "Ophidia") as the supra-temporal, and not the squamosal as do Huxley and his followers.

[1] Boulenger, G. A.: Ann. & Mag. Nat. Hist. (ser. 6) vol. xi. 1893, p. 209.

[2] Baur, G.: Anat. Anz. Bd. x. 1895, p. 322, *cf.* also Amer. Nat. vol. xxx. 1896, p. 145.

[3] Dollo, L.: Bull. Mus. R. Nat. Hist. Belg. t. ii. 1883, p. 235.

[4] Baur, G.: Zool. Anz. Bd. ix. 1886, p. 685.

[5] Baur, G.: Journ. of Morphol. vol. iii. 1889, p. 473.

temporal arch of the Squamata represents only the upper arch of the Rhynchocephalia, basing his conclusions on the surmise that the quadrato-jugal is not unrepresented in the former as is usually supposed, but that the bone generally termed the "squamosal" is its homologue. Somewhat similar conclusions follow from the later determinations of Gaupp, laborious but unconvincing, in which he seeks to show[1] that the bone hitherto known as the quadrato-jugal in Batrachia and Birds must be for the future termed the "quadrato-maxillary," and that for the quadrato-jugal in Crocodilia, Chelonia, Rhynchocephalia, and Lacertilia, the term "paraquadrate" must be employed.

Baur assumes that the Squamata "never possessed an infra-temporal fossa, but that the broad arch was reduced from below in the same way as in the Testudinata" (*op. cit.* p. 473). It is beyond the scope of this memoir to fully discuss this question, voluminous in itself, but there tells strongly against the interpretation of the bone which in the "Squamata" reaches the head of the quadrate with that which in the Rhynchocephalia flanks its lower articular border, the fact, long ago pointed out by Huxley[2], that in the living Lacertilia there is present a ligament having the relationships of the latter. And, further, argument by analogy to the living Urodela, in which, while the maxillo-jugal arch is complete in bone only in the Eastern genus Tylototriton[3], a similar representation is present in ligament which may extend even into the maxillary region, places a further obstacle in the way of its acceptation. All recent investigation has gone to show that the Reptilia and the Batrachia are the diversely modified descendants of the Stegocephalia; and the fact that in them the supra-temporal, squamosal, and quadrato-jugal coexist in a transverse series tells with great force against this seductive argument.

The "Septo-maxillary."—This bone was originally described in Sphenodon by Osawa (98[a]. p. 503) as a small semicircular element attached by fibrous tissue to the vomer, and he therefore named it a "turbinal." In this he was unquestionably in error. The bone was figured and described by Parker in Zootoca[4] as the septo-maxillary, and under this name it has been more recently described by Gaupp in other lacertilian embryos. Concerning its detailed relationship, he associates it with the support of the septum nasi internally and with that of the border of the cartilage enclosing Jacobson's organ superficially (*op. cit.* Ber. p. 10). The bone present in Sphenodon (Pl. IV. fig. 2, *s.mx.*) is still more superficial in position and free of the nasal septum than this. In consideration of the fact that whereas here the Jacobson's organ is completely roofed in cartilage, in the lizard, according to Parker, the septo-maxillary fulfils that function[5],

[1] Gaupp, G.: Morphol. Arbeiten, Jena, Bd. iv. 1895, p. 77.
[2] Huxley, T. H.: Anat. of Vertebr. 1871, p. 190.
[3] Riese, H.: Zoolog. Jahrb., Anat. Abth. Bd. v. 1892, p. 99.
[4] Parker, W. K.: Phil. Trans. 1879, pt. ii. p. 609.
[5] Parker, W. K.: Phil. Trans. 1879, pl. 44. fig. 5.

we are disposed to regard the bone as its homologue. It is figured in the macerated state at Pl. VI. fig. 1, *s.mx.*, and, as remarked by Gaupp, is a membrane-bone.

The supposed "lachrymal" of Günther (67. p. 597), accepted by Hofmann [1], Seeley (?) [2], and Credner [3], has no existence.

The Præ- and Postfrontal and Postorbital.—The two former are proved by their development to be membrane-bones [4], and examination of Pl. IV. fig. 10 shows that they are neither of them compound and that there are no correlated chondro-cranial ossifications.

The postorbital has the customay relationships of that bone and is very large [5].

[1] Hofmann, C. K.: Bronn's Klass. u. Ordng. d. Thier-Reichs, Bd. vi. Abth. 3, pl. 66. fig. 5.

[2] Seeley, H. G.: Journ. Linn. Soc., Zool. vol. xii. 1876, p. 184. "In front is a small lachrymal, which is not found in Chelonians." The context is not clear.

[3] Credner, H.: *op. cit.* p. 510. Baur has pointed out the error here, Amer. Journ. Sci. vol. xxxvii. 1889, p. 311.

[4] We retain the term præfrontal, as one now in general use. It is, however, unfortunate (since it was originally applied by St.-Hilaire, in 1807, to a cartilage-bone, which Cuvier in his 'Leçons' defined as transmitting the olfactory nerve) that it should have become applied indifferently to various cartilage and membrane bones occurring in the præfrontal region. A great confusion exists with respect to the modern usage of the term, but it does not materially affect our work.

[5] The study of the postorbital in Sphenodon is intimately bound up with Günther's work upon the living Crocodilia, which possess but a single so-called "postfrontal." On the basis of comparison with this he came to regard the postorbital of Sphenodon (which, following Stannius, he termed "quadrato-jugal") as "a detached portion of the postfrontal" (67. p. 598). Baur discovered in 1886 (Zool. Anz. Bd. ix. p. 740) that both postfrontal and postorbital are present in Belodon, and accepted Günther's conclusion concerning Sphenodon. Their reasoning suggests an origin of the postorbital from the postfrontal, rather than that both bones were originally distinct, and that the presence of one or both is due to variation by co-ossification with age. And, as bearing upon this, we submit the following observation:—Cuvier showed that in the Iguana ('Leçons,' t. x. p. 14) there are two bones occupying the region of the postfrontal of other Lizards. He applied to both this term, and figured them as attached side by side to the postorbital process of the frontal. In our own example the hinder bone alone has this relationship, the former being pushed forwards in front of the process named. Comparison with the single "postfrontal" bone present in many Lizards—*e.g.*, the familiar backwardly-pointed bone of Varanus—shows this to have the detailed relationships of Cuvier's two "postfrontals" in Iguana, wherefore suspicion arises that it is perhaps compound. That this may be the case is proved by the skull of a young Tupinambis in our possession, in which, as Mr. M. F. Woodward has shown us, two bones are present in its place. Contrary to what happens in Iguana, the postfrontal is alone attached to the frontal and the postorbital to it. This notwithstanding, it follows that the bones described by Cuvier in Iguana are the postfrontal and postorbital, and that they are both represented in the varanoid type (*cf.* also Gaupp on the embryo Lacerta, in Morph. Arbeiten, Bd. iv. p. 77, pl. vi. fig. 9). We are also indebted to Mr. Woodward for drawing our attention to a skull of the Green Turtle (Chelone mydas) in our Teaching Collection, in which that portion of the "postorbital" suturally connected with the anterior two-thirds of the frontal is on the left side distinct—*i.e.*, an independent postfrontal is present.

These facts go far to prove that in the Reptilia generally, where either a single "postfrontal" or "postorbital" is alone present, it may be a compound of these two; and they certainly suggest that the postfrontal of the living Crocodilia may have gone elsewhere than over to the frontal, as surmised by Baur.

The Mandible.—The mandibular ramus has been shown by Baur to consist (95ª. p. 413) of the six elements usually present in that of other Reptilia. He originally described it in 1891[1] as resembling most closely that of those Chelonia in which the angular and supra-angular, apposed behind the splenial, under-arch the articular, and as destitute of the 7th element or "præsplenial" described by him in these animals. We have only to add that at the latest stage observed by us (T) the articular has not yet appeared, the articular region being still cartilaginous, and that at Stage S the angular and supra-angular (*s.a.*, Pl. IV. fig. 4) are still separated by the splenial (*sp.*).

6. The Appendicular Skeleton.

The Pectoral Girdle.—Concerning this we have little to record. The simplicity of the coracoid was pointed out by Günther, in the remark (67. p. 611) that it has "no notch whatever." Fürbringer, in a passing allusion seven years later[2], commented on the rounded border and feebly ossified state of this (Pl. VI. fig. 6, *cor.*), and there can be no doubt that in respect to these features it simplifies the Lacertilian type. As pointed out by Fürbringer, however, the Chamæleons approximate to a similar condition, but it may be questioned whether the "simplification" in them is not due to secondary causes. Ossification takes place during Stages S and T, on lines common to both the Batrachia and Reptilia. An interesting detail is the early appearance of the clavicle, viz. at Stage Q (Pl. VI. fig. 4, *cl.*), at which no cartilage-bones are anywhere present in the axial skeleton. The interclavicle appears later. We have failed in all attempts to find evidence of a cartilaginous predecessor of these bones.

The relationships to the sternum we have already described (*antea*, p. 33).

The Pelvic Girdle.—Günther accurately described the adult girdle, except that he applies to the ileo-pectineal process the term "uncinate" (67. p. 615). Like the shoulder-girdle, it is at Stage Q fully chondrified. Its two halves (Pl. VI. fig. 7) are united, and there is a considerable cartilaginous symphysis (*c.i.p.*) which in the mid-ventral line separates the cordiform fenestræ (*f.c.*). With later growth (at Stage R) a backwardly-directed median process (the hypoischium of Mehnert[3]) becomes conspicuous, but it is never segmented off or ossified to form an "os cloacæ" as in Lacerta. The epipubic cartilage (*e.*) like it is simple—*i. e.*, there is nothing to suggest those processes of bifurcation and subdivision recorded for certain Lacertilia.

Interest attaches to the ligamentum medianum pelvis, from the fact that while Wiedersheim has described[4] in its place in the adult a cartilaginous tract uninter-

[1] In his 1895 notes he admits a transposition in those of 1891 of the terms angular and splenial, but it does not affect his comparison.

[2] Fürbringer, M.: Morph. Jahrb. Bd. i. 1876, p. 643.

[3] Mehnert, E.: Morph. Jahrb. Bd. xvii. 1891, p. 123.

[4] Wiedersheim, R.: Zeitschr. wiss. Zool. Bd. liii. 1892, p. 54.

ruptedly continuous with the epipubis and hypoischium, Mehnert has denied (*op. cit.* p. 142) a "skeleto-vicarious" significance to this ligament for Lacerta. Our developmental material shows that Wiedersheim was in error, since the ligament is already present (Pl. VI. fig. 8, *l.i.p.*) at Stage R. Concerning Mehnert's conclusion, we can only add that in Sphenodon the ligament is preformed in cartilage (Pl. VI. fig. 7, *c.i.p.*) at first of considerable extent, and that with advancing development, correlatively with the expansion of the pelvis and widening of the cordiform fenestræ, this undergoes a relative reduction with accompanying replacement in fibrous tissue. If Mehnert is correct, the cartilaginous symphysis and the primarily small size of the fenestræ carry Sphenodon so much nearer the Batrachia.

In the course of our work our attention became arrested by the fact that there are apparently two types of hip-girdle represented in the adult. We append camera-lucida figures of these. When viewed from beneath, it is evident that the essential difference

Fig. 13.

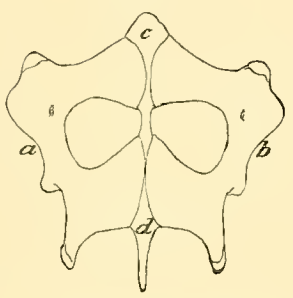
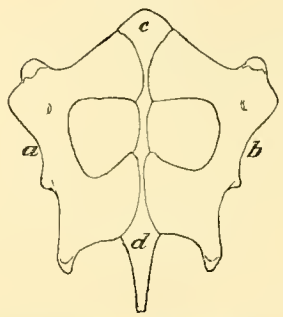


Fig. 14.



Camera-lucida outline sketches of extreme types of the adult pelvis of *Sphenodon*.
13, least expanded; 14, most expanded. Nat. size.

between them is one of increased length as compared with breadth. In the pelvis of the least expanded type (text-fig. 13) the cordiform fenestræ are more rounded than in the most expanded, in which they appear (fig. 14) angular; and we find that whereas in the least expanded type the transverse measurement across *a–b* is about equal to that along *c–d* (fig. 13), in the most expanded (fig. 14) *c–d* is greater. We note, however, that in all cases the distance between the opposite limits of the cordiform fenestræ is equal to that of the symphysis ischii from the vertebral column and to the transverse diameter of the sacrum.

For want of material undoubtedly mature upon which to base further comparison, we are unable to decide how far this is or is not a sexual matter; but we are disposed to believe the contrary. The only other case known to us, which is at all analogous, is that of the presence of two still more distinct types of scapulæ in an extensive collection of bones of the Australian Dugong brought home by Professor Haddon, F.R.S., from Torres Straits in 1889, now in the custody of one of us.

The Long Bones.—Under this head we include the humerus and femur, radius and tibia, ulna and fibula. They have all been so often described, from Günther to Osawa, that detailed recognition by us would be superfluous. We would only add that the condylar foramina of the humerus, originally observed by Dollo (84), are both fully formed at Stage Q (Pl. VI. fig. 10, *f.en.*, *f.ec.*), and that the inner has from the first period of differentiation its canal-like character.

The long bones are the first of all the cartilage-bones to ossify.

Carpus and Tarsus, with Phalanges.

It is evident, from the study of both carpus and tarsus, that chondrification sets in correspondingly (for the tarsus, *cf.* Pl. VI. fig. 15). One inexplicable feature is the long duration of the cartilaginous state of both. Ossification begins in both postaxially (as is seen in fig. 14 for the carpus), but not until the rest of the limb is fully ossified.

We have examined both carpus and tarsus at all stages of development back to Q, where these elements are first chondrified. To make sure of detail, we have employed, beyond clarified dissections, serial sections cut horizontally.

The Carpus.—Günther described ten carpal elements, and in this he has been followed by others. He appears to have missed one of the centralia, and to have confused the other with the proximal elements, which he describes as five in number (67. p. 612). Osawa, the latest writer on the subject, correctly records eleven elements (98[a]. p. 528), the eleventh being the secend centrale, detected by Bayer (84. p. 237), who first applied to the parts a rational terminology. It was, however, independently discovered by Dollo and Baur (86[a]. p. 188), the latter opposing Bayer's conclusion that its supposed absence is due either to disappearance or union with another carpal element. In this he was right, for we find it always present.

None of the afore-mentioned observers describe the precise size and relationships of the two centralia to each other and the adjacent carpal elements. Osawa, however, gives a very different delineation to the dorsal and ventral aspects of the same pair, and figures the præaxial as outwardly extended between the radiale and first carpale as seen from the dorsal surface (98[a]. p. 527, figs. 13 & 14). While we can confirm the accuracy of this, we are able to record further suggestive details. From a comparison of our figs. 12 and 13 (Pl. VI.) which represent the opposite carpales of the same individual, we find that the right (fig. 12) is normal but that the left (fig. 13) is exceptional, in the fact that the præaxial centrale (*pr.c.*) is smaller than the postaxial (*po.c.*) and lies wholly between the radiale and the first carpale, instead of merely extending between them. The postaxial centrale, on the other hand, is correspondingly enlarged, whereby it articulates with the second carpale, as well as with the third and fourth, to which alone it is usually related. There is thus to be observed an inverse

proportion to that of the corresponding centralia of the other limb (fig. 12). Bayer has suggested that in the presence of the double centrale Sphenodon exhibits a Batrachian tendency, drawing attention to the great extent to which the living Urodela are doubly centralial. One of us has, with another, attempted to show[1] that the presence of a second centrale carpi is a diagnostic character of the Anura, and this goes to support Bayer's argument. As to centralia, however, Wiedersheim has demonstrated[2] the presence of three in the Axolotl; and with these facts in mind it occurred to us that the inequality in development of the two centralia in Sphenodon might possibly be due to the presence of a third, which had fused with the opposite fellow on the opposite sides in the pair of limbs under discussion. At Stage Q the condition of the centralia was found to be the same as in the normal adult; but in a young specimen belonging to the R. College of Science, Dublin, the præaxial centrale is on each side ossified from two independent centres (Pl. VI. fig. 14, *pr.c.*), and in such a form that while co-ossification of them would bring about the condition of the right limb (fig. 12), co-ossification of the middle nucleus with the postaxial centrale (*po.c.*) would result in that of the left.

Bruhl, for some unaccountable reason, systematically terms[3] the pisiform of Reptiles the "ulnar sesamoid"! Concerning the rest of the proximal carpals and the centralia we have nothing to add.

The distal carpals, stated by Günther to be five in number, are by Bayer enumerated as four. As he was dealing with a young animal he found only the 4th carpal ossified. This is seen to be the case on the left side of our figs. 12 and 13, in which (Stage T) the rest of the carpus is still cartilaginous (*cf.* previous statement on p. 60). Bayer believed that the 5th carpale is to be sought in the cartilaginous head of the related metacarpal (*op. cit.* p. 241); but in this he was mistaken, as pointed out by Baur in that it is always present and distinct, though small (Pl. VI. figs. 11 to 14).

We have no variations or other matters to record concerning the phalanges of the fore limb.

The Tarsus.—Günther describes two proximal and two distal elements, and is doubtful about a fifth—the fifth tarsal. He alludes without name to the "meniscus" of Born, which we figure (Pl. VI. fig. 18, *mn.*). Osawa describes one proximal element, the "proximal tarsale," and four distal—five in all. He regards the meniscus (p. 504) as the first tarsale, while Born associates it in the Lacertilia[4] with the centrale. Both are in error, for whereas the meniscus does not appear till Stage S (when all the tarsal elements have been formed), the first tarsal arises at Q (fig. 16) as a separate element (I.), and at Stage R, when fully chondrified, unites with its metatarsal. The meniscus is thus proved to be an accessory element (*cf.* Born, Morph. Jahrb. Bd. vi. 1880, p. 67).

[1] Howes & Ridewood: P. Z. S. 1888, p. 177.

[2] Wiedersheim, R.: Morph. Jahrb. Bd. vi. 1880, p. 581.

[3] Brühl, C. B.: Zootomie aller Thier Kl., Wien 1880, pls. 31–34 and 53 & 54.

[4] Born, G.: Morph. Jahrb. Bd. ii. 1876, p. 25.

Born, as is well known, gave it as characteristic of the Lacertilia that tarsalia 1 and 2 were probably united with the corresponding metatarsals; and in this he has been followed by Bayer (p. 243), who claims a phylogenetic union for these! Osawa rightly figures the second tarsale of Sphenodon as distinct; and we find that from Stage Q (fig. 15) to the adult state this is present as an independent element (as in fig. 18) which becomes extensively ossified.

Perrin asserts (95. pp. 44 & 97) that five separate distal tarsalia are present, and his figure 9 may illustrate but does not adorn his text! We are at a loss to understand what he has figured; but one thing certain is that in ascribing three phalanges to the fifth digit he is in agreement with Bayer, who is inclined to regard the hooked bone, which by its angulated head articulates with the outer face of the fourth tarsale, as the fifth of that series. As a salient objection to regarding this as a metatarsal he seeks to show that on the Güntherian determination Sphenodon would be an exception to the rule among Lizards in possessing more than three phalanges to the fifth digit; but it does not occur to him that this statement is tantamount to admitting that the angulated bone is in most Lizards a metatarsal, and that it thereby nullifies his argument. Dismissing for the moment the facts of development, the discovery by us that a specimen preserved in the R. College of Surgeons Museum is possessed of three phalanges on the outermost digit of one hind limb, and four on the other, dispenses with the necessity for further discussion of this point, except to remark that among the Chelonia, Pleurodira (Emydura) for example, we meet with a quadriphalangeate fifth toe. The matter is clearly one lying within the range of individual variation.

Developmentally, this bone, angulated from the first period of its differentiation (Stage Q, Pl. VI. fig. 16, *v.*), ossifies at R (Pl. VI. fig. 17), at the same time and in the same manner as the other metatarsals; and we have already pointed out that the tarsal elements do not ossify until T, when the metatarsals are formed. And were further proof needed of its metatarsal homology, it is forthcoming in the totally different manner of ossification of the carpus and tarsus and the metacarpals, metatarsals, and phalanges—the former ossifying endosteally, the latter ectosteally.

There is no trace in Sphenodon of tarsale 5 actual or potential, and no evidence developmentally for the belief of Baur that it is incorporated in the fourth tarsale (Zool. Anz. Bd. ix. p. 189)[1]. It seems to have vanished even from the ontogenetic record.

Concerning the proximal tarsal series, Osawa describes one confluent element; and Günther evidently had to deal with a specimen in which they were just uniting, for the "suture" to which he refers as "scarcely visible" is recognizable, as in our Pl. VI.

[1] We are disposed to believe, with Forsyth Major (Trans. Linn. Soc., Zool. vol. vii. 1899, p. 510), that the compound nature of the "cuboid" is seriously open to doubt.

fig. 18, in all but old individuals. Bayer, finding the præaxial moiety of the "astragalus" cartilaginous, regarded it as the tibiale, and the whole "astragalus" as consisting of the centrale [1] and the intermedium, the "calcaneum" being to him the fibulare (*op. cit.* p. 243). Perrin, going further, names the "astragalus" (*op. cit.* p. 44) the "tibio-centro-intermediare."

Development at Stage Q shows (Pl. VI. fig. 16) that at the chondrification period the "astragalus" and "calcaneum" are independently chondrified, and a feeble ypsiloid differentiation (accurately indicated in the fig.) may be observed at what would be the apposition lines of the tibiale (*t.*), centrale (*tc.*), and intermediare (*i.*), were they distinct. In an earlier embryo of the same stage (fig. 15) we found the intermediare (*i.*) and fibulare (*f.*) chondrified and separated by a foramen apparently homologous with that known as the f. arteria perforans mesopodii (*fb.*), the centrale (*tc.*) and tibiale (*t.*) being procartilaginous, although in close apposition with the intermediare and with each other. Bayer and Perrin had correctly surmised!

7. The Dentition.

The detailed study of the tooth-genesis does not fall within the scope of our work, but we have one or two interesting anatomical facts to record.

Firstly, as to the vomerine teeth. No trace of them in a calcified form is forthcoming up to Stage T, the oldest we have examined. We can add nothing to what is recorded in the latest account given by Siebenrock [2]. It may be that we have not happened to deal with embryos in which they were developing, or, perhaps, that these clearly vestigial organs attain their full development late.

Baur would seem to be wrong in the surmise (96[b]. p. 437) that they exist in young specimens and disappear in old age [3].

The Incisors.—These have been correctly shown by Dendy (99[a]. p. 77) to be represented in the young stage by three pairs of "distinct pointed conical teeth" above and below, and not by two as believed by Günther (67. p. 602) and Baur (p. 436). It is worth remarking, however, that Knox had already recorded the supposed existence of three pairs in the upper jaw (69. p. 18), and Newman in the lower (77. p. 234), the former stating that they were confluent at their bases. This is the case at our Stage T

[1] Baur's passing remark (Zool. Anz. Bd. ix. p. 189) that he found this represented by a piece of cartilage which was "eingekeilt" is suggestive of begging the question.

[2] Siebenrock, F.: Transl. cit. p. 399.

[3] Further search is necessary to ascertain how far the vomerine teeth are or are not represented during ontogeny, and a former pupil of mine, Mr. H. Spencer Harrison, has undertaken to immediately work out this and other problems connected with the dentition of Sphenodon as the subject of a special communication to appear in the Qu. Journ. Microscp. Science.—G. B. H.

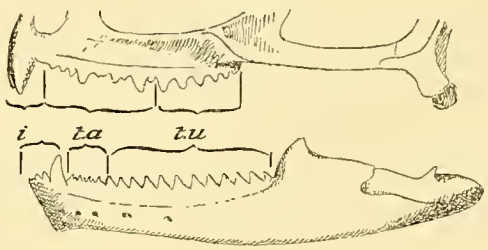
(Pl. II. fig. 15), the outer tooth of each set being somewhat the larger of the three. At Stage S (fig. 14) all are seen to be free, and the outer still large. Beyond the mere inference of fusion, Dendy does not state the method by which he presumes these pointed incisors to be converted into the tusks of the adult. As a rule each of the upper tusks, when fully formed, is doubly pointed (or, as remarked by Günther, "notched") (*cf.* text-fig. 15), there being a smaller internal cone, and a larger external one somewhat backwardly curved (text-fig. 16). In the lower jaw there are three cones (text-fig. 16), a larger external and two smaller internal, the three teeth which are

Fig. 17.

Fig. 15.

Fig. 16.

Fig. 18.



Illustrations of the dentition of *Sphenodon*.

Fig. 15. Incisors, front aspect, old individual. Fig. 16. The same, younger individual, little worn. Both nat. size. Fig. 17. Enlarged sketch of upper incisors of fig. 16, × 6. Fig. 18. Complete adult dentition: nat. size. *i*, incisors; *t.a.*, cheek-teeth, alternating series; *t.u*, cheek-teeth, structurally uniform series.

present having united with the mandible. That portion of the dentary element which bears them becomes, with them, clothed in an enamel-like substance, which justifies Günther's remark (67, p. 602) that the alveolar edge of the mandible is polished. Tomes [1] regards this substance as true bone.

In the embryonic upper jaw the middle incisor present early ceases to elongate (*cf.* Pl. II. fig. 15, *t.m.*) and at Stage T it becomes loose. The reason of this is evident from the fact that longitudinal section (Pl. II. fig. 16) shows it to be confluent

[1] Tomes, C.: Dental Anatomy, ed. 4, 1894, p. 253.

only externally with the premaxilla (*p.x.*) and not by its whole base, as is the case with the other teeth. We suspect that this tooth is early shed, but unfortunately our material does not embrace a specimen proving the point.

A possible source of error must not be here overlooked, in the fact that in the adult there may be present a small pointed cusp (text-fig. 16, *) between the two upper incisors, which at first suggests a persistent middle tooth. When, however, a tooth thus constituted is examined under a lens, it is found that the minute cusp has a counterpart (text-fig. 17) on the inner face of the inner tooth, and that, like this, it is but the product of its base. And since the teeth, when first formed, are simple cones, these lesser cusps must be due to secondary complication.

The palatal and maxillary teeth vary very greatly in appearance at different stages in development and periods of life. One conspicuous feature which has not been recorded is that at Stage S the maxillary teeth number 11 and the palatal 4-5 (*cf.* Pl. IV. figs. 4–6). These first-formed cheek-teeth usually alternate, a larger and a smaller occurring in succession, and not infrequently they may be arranged in recurring sets of three, a larger and two smaller to each. At Stage T the same numerical condition obtains (allowing for individual variation, most marked for the palatine teeth), but under the growth-processes at work the larger teeth have now increased in size. From this period onwards the numerical increase in the teeth as a whole is due to superaddition from behind forwards, and most of the teeth thus formed (*t.u.*, text-fig. 18) are uniform in size. Numerically they average about 6 on either side, and for the palate about 4–5, giving a total number of about 16–17 maxillary teeth and 9–11 palatal [1].

Passing to the mandibular series, we note an essential similarity to the maxillary, in the arrangement of the teeth first formed. At Stage S (Pl. IV. fig. 4) there are 11 alternating teeth as in the maxilla [2], but no others. On the assumption of Stage T the teeth of the alternating series, unlike those of the upper jaw, apparently cease to grow. Wear and tear supervening, and the development of the structurally uniform teeth continuing apace, these (*t.u.*, text-fig. 18) become predominant; and hence the condition herein delineated, which is of short duration, as the teeth of the alternating series (*t.a.*), now insignificant, become rapidly worn down.

Baur has described (95[b]. p. 436) a Sphenodon skull, 25 mm. in length, having two

[1] The number of teeth recorded by different observers ranges for the maxillary from 6 (Knox) to 17 (Colenso), and for the palatal from 5 (Knox) to 13 (Newman); for the mandibular from 13 (Colenso) to 19 (Günther). In the absence of detailed description and knowledge of degree of wear and tear, it is not possible to make use of these figures.

[2] This alternation is a striking feature. Among the Monitors it is often the case that in the fresh state the cheek-teeth are similarly, though more markedly, alternate, the elongated teeth being fixed to the jaws alternately with small ones which are freely displaceable at their bases. Can it be that there is a common determining cause at work here?

upper incisors and an eminence which he surmised suggested a third, and he remarked [1] that each of the inner incisors on either side had a very small successional tooth, which he believed was never further developed. On examination of a series of sections of a 19 mm. example we find a similar tooth (Pl. II. fig. 16, *td.*) but behind the middle tooth of the three that are present (*t.m.*). Baur's specimen appears to have suffered the loss of the middle incisor, and to justify our conclusion that this is shed. And while we are not sure whether our successional incisor is the same as his, or whether he and we were dealing with members of a series which may be formed, his conclusion that the tooth is never functional receives support from what we have observed [2].

In describing the cheek-teeth, Baur attributed to the fifth maxillary and the first mandibular a successional tooth. This we have not been able to confirm. Passing to the structurally uniform series (*t.u.*), we find these to mostly arise lineally. Pl. II. fig. 17, in its outlined portion, is a reconstructional drawing from horizontal microscopic sections at this period. The teeth drawn in outline (*t.f.*) are fused to the maxilla and palatine, as indicated. Those drawn in colour, together with the shaded portion of the drawing, are from individual sections, the teeth which appear to represent the structurally uniform series (coloured yellow) being delineated in the position in which they arise.

The teeth of the adult Sphenodon have been defined by Günther (67. p. 601) as "acrodont in the strictest meaning of the term." Boulenger (Brit. Mus. Cat. cit. p. 1) regards them as "not implanted in alveoli"; while Tomes, ignoring the incisors, has written of the post-incisors that they are "acrodont," and he further suggests that the glistening investment of the alveolar edges, which Günther originally described and showed to "perform the functions of teeth when these are ground down . . . . . in advanced age," is true bone. Baur refers (p. 437) to "alveoli" in his 25 mm. specimens, but gives insufficient details.

If we may infer from the foregoing that Tomes, ignoring the incisors, was suspicious of their being in the adult non-acrodont, we have to confirm his doubts. Thanks to Mr. M. F. Woodward, we have been enabled to examine a series of microscopic sections of both upper and lower incisors of the adult *in situ*; and concerning the upper there is evidence of surrounding bone—not as the result of a truly thecodont condition, but of an apparent secondary overgrowth subsequent to the union between tooth and jaw. Examination of Pl. II. fig. 18 shows in the case of a mandibular tooth that the truly acrodont condition is assumed at Stage S; and at Stage T the incisors show in our sections a condition intermediate between this and that above described. Further investigation of this topic is beyond the limits of our pledge to Professor Dendy, but, pending detailed study of the tooth-genesis, we would distinguish the condition occurring in at least the incisors as *hyperacrodont*.

[1] As usual, he writes (line 8) "innere" for "aussere."

[2] We have no material to show whether the embryo teeth which we herein describe do or do not become later replaced.

8. Summary and Conclusions.

Summary.—The following is a summary of the more important conclusions embodied in Sections 5 to 7 of the present Memoir:—

1. That two kinds of intercentra are formed: primary intercentra, originally paired and mostly preformed in cartilage; and secondary intercentra, which replace those throughout certain regions of the body, and are mostly median and arise by direct ossification outside the vertebral column.

2. That the primary intercentra persist in the caudal region to form the chevrons, and anteriorly for the first few segments, and that the secondary intercentra coexist with them in the anterior caudal region alone.

3. That the hyaline cartilages which go to form the vertebral centra are paired in origin.

4. That an intravertebral chordal plate is formed by transformation of the substance of the chorda within each vertebral centrum, and that the plate is continuous with the chordal epithelium, which becomes converted into a tunica lying inside the chordal sheath.

5. That during the final differentiation of the vertebræ the chorda becomes metamerically segmented, and that there appears in each segment a central chordal vesicle at the point of greatest flexibility.

6. That in that part of the caudal region modified for "splitting" there are formed, by similar differentiation to that which gives rise to the intravertebral chordal plates, a series of intervertebral plates, and that the intravertebral plates play an important part in the casting of the tail, and may be possibly the seat of regenerative activity in the formation of the renewed caudal axis.

7. That the ribs arise in procartilage, in relation to the primary intercentra, with which they are the first differentiated skeletal elements; and that they are differentiated obliquely, the capitular portions in direct relationship with the intervertebral regions and the intercentra—the tubercular with the areas of differentiation of the vertebral centra and arches of the vertebræ behind. That these relationships are lost during later development for all but the third and fourth præsternal segments.

8. That the uncinates are separate in origin, with the possible exception of those of the penultimate and antepenultimate præsternal ribs.

9. That the cartilaginous brain-case is a product of the union of distinct ethmo- and orbito-sphenoidal plates, and that its bars and fenestræ are all attributable to direct processes of growth—*i. e.*, that it is not a fenestrated cranium of the cartilaginous fish type.

10. That the hypoglossus nerve-bearing region bears five pairs of nerves with four pairs of foramina, and that during development these become reduced to two each.

11. That the trabeculæ cranii play no part in the direct formation of the lateral cranial wall, and that they represent a pair of præoral visceral arches.

12. That the epipterygoid bone is the product of ossification of the ascending process of the pterygo-quadrate cartilage, and that the special feature of the quadrate bone is an extension of its ossific head into the latter for approximation to the epipterygoid.

13. That the columella auris and stapedial processes are alike direct derivatives of the hyoid arch, with which they are continuous at all stages, and that structural complication is due to overgrowth of the same.

14. That the upper end of the hyoid cornu is attached to the quadrate only, and that there is a fleeting "jointing" of the former throughout its course.

15. That in the meeting of the pterygoids and vomers, the latter play a part leading up to the conditions occurring in the Chelonia and Plesiosauria.

16. The cartilaginous pterygo-quadrate is in its detailed characters most nearly comparable to that of the Apodal Batrachian Ichthyophis.

17. That each of the three segments of each of the "abdominal ribs" (gastralia) arises by union of a number of calcifications, and that the median segment may be paired. That the "plastron" is present in a degenerating form.

18. That in their early differentiation the membrane-bones of the head and face are predominantly circumorbital in position.

19. That there is no supratemporal bone recognizable at any stage as a distinct element.

20. That the hip-girdle in its development is of a lower type than the Lacertilian, and that there are two types of pelvis present in adults.

21. That the fifth tarsale has no existence in ontogeny, and that the basal element of the fifth digit of the hind limb is a metatarsal.

22. That there are apparently three centralia carpi represented during development, and that a centrale is incorporated in the "astragalus."

23. That calcified vomerine teeth are not present during encapsulation within the egg-shell.

24. That of the three pairs of upper incisors, the middle certainly disappear and the inner may become tricuspid.

25. That the cheek-teeth appear to consist of two series—an early developed alternating set, and a later posterior and structurally uniform set.

16. That there arise within the occipital region and the individual vertebral segments sustentacular ligaments, for support of the medulla and spinal cord.

Conclusions.—Paragraphs 16, 17, 20, and 22 of our Summary add fresh testimony to the belief in the Batrachian affinities of the living Sphenodon, while paragraph 15 strengthens the demonstration of its Chelonian resemblances and extends these to the Plesiosauria. Paragraph 17 proves the creature to be a highly modified representative of its Suborder, but at the same time to pass through a developmental phase realistic of the lower Suborder of the Rhynchocephalia, as now classified; and the same is true of paragraph 24, by comparison with the Proterosauria (especially Palæohatteria). Of the supposed Agamid affinities we have written enough (*antea*, pp. 4, 22, 46).

Sphenodon, judged from our standpoint, must be regarded as the surviving representative of that group of animals ancestral to all the living Sauropsida, and to at least the Dinosauria, Pterodactyla, and Ichthyosauria, of the past—if not of the Mosasauria and Dolichosauria also, and unquestionably intimately related to the Anomodontia. As concerning the unmistakable Stegocephalian affinities of the Rhynchocephalia, it becomes necessary to enquire more closely than hitherto into the sum of those characters which constitute a Batrachian a Batrachian—a Rhynchocephalian a Reptile.

Attention was in 1892 called by one of us (Journ. Anat. & Phys. vol. xxvi. p. 402) to the fact that whereas no Batrachian living or extinct was then known to possess more than two phalanges on each of its two innermost digits—the formula for the Class being 2 2 3 4 2, that of the Sauropsida being 2 3 4 5 4 (or something minus that by reduction), it would seem impossible to derive the Sauropsidan condition from that of any known Batrachian, not excluding the Stegocephalia. Recent investigation, however, has modified this aspect of the question. Firstly, there has been discovered an undoubted Stegocephalian ally having on the second digit of its fore limb three phalanges and on the third four, and for its hind limb the formula 2 3 4 4 3 [1]. And, again, in Credner's *Sclerocephalus* of the Permian, which, its massive quadrate notwithstanding, he places among the Stegocephalia [2], there existed a combination of the lowest Stegocephalian type, amounting, in the structure of its dermal skeleton, almost to the "Ganoidan," with a limb-skeleton (if the remains are rightly associated) of a veritable lizard—the phalangeal formula being 2 3 4 5 4 for the hind limb, and that clawed [3].

Again, as to the sternum, it has also been pointed out by one of us ('Nature,' vol. xlviii. p. 269, 1891) that a sharp distinction may be drawn between the *coraco-sternum* of the Batrachia (*an archisternum*) and the *costal sternum* of the Amniota (*a neosternum*), the existence of which in any Batrachian or Stegocephalian has not been proved.

And as to the skull, the now well-known fact that whereas in the Amniota the hypoglossal nerve-bearing region, truncal in origin, is incorporated in the occiput, in the Batrachia these nerves are postoccipital [4], once again opens the gap between the Batrachia and Amniota—indeed, so markedly, that our ideas may be systematized by

[1] Ceraterpeton galvani, A. S. Woodward, Geol. Mag. (dec. 4), vol. iv. p. 297 (1897).

[2] Credner, H.: Zeitschr. deutsch. geolog. Gesellsch. Bd. xiv. 1893, p. 639.

[3] We are at a loss to understand the reason for the intercalation in the restored portions of the skeleton of *Pariasaurus* in the British Museum of Natural History of a fourth phalanx to the second digit of the hind-limb, especially as in the original description of the specimen it is the front-limb of which it is said (Phil. Trans. vol. 183, B. p. 363) to be possible that one digit may have had four! We fail to discover evidence of more than three phalanges for any digit that is preserved.

[4] Restricting the terms to the Terrestrial Vertebrata, we leave aside the question how far the vagus-bearing portion of the skull may be truncal also, and that of the undoubted parallelism which exists between the Amniota and certain Ichthyopsida, concerning the union of skull and vertebral column (*cf.* the masterly Memoir by Fürbringer, M.: Gegenbaur Festschrift, Leipzig, 1897).

applying to the former condition the term *Archicraniate*[1], and to the latter that of the *Syncraniate*.

The characters of the occipital condyle and the presence of one, two, or, for the matter of that, of three condyles, no longer have the significance once attached to them as criteria of affinity.

Judged from this point of view, the Rhynchocephalia may well be regarded as a lowly group, ancestral to the Sauropsida as ordinarily defined, and intimately related to the Anomodontia; and while the latter, perhaps with or through the Pelycosauria of Cope, on the one hand gave rise to the Mammalia, they were probably with the Rhynchocephalia derived by diversity of modification from some common ancestral stock which carries us towards a group which must have been either Batrachian Reptiles or Reptilian Batrachians, as compared with forms extant—*i. e.*, they either possessed a coraco-sternum and an archicranium, or a costal-sternum and a syncranium, structural combinations which go hand in hand. If they were of the latter type, the living Batrachia must have suffered the loss of a costal-sternum and not a few of their distinctive characters must be indicative of retrogression. The argument applies equally to the quadrate and whether its representative in the living Batrachia is or is not vestigial, and, as concerning the parasphenoid and pterygoids, the question arises whether in these ancestral forms they did or did not reach the vomers.

On the other hand, it is possible that, in some manner yet to be discovered, the ancestral series of Terrestrial Vertebrata may have combined the characters of the later differentiated forms, as Gadow has surmised in his sagacious remark[2] that "the Amphibia and Reptiles do not form a continuous line of development, but are two divergent branches of a common stock of Palæozoic Tetrapoda." If, with Credner, we group together the Stegocephalia and "Proganosauria" as the "Eotetrapoda"[3], or with Dawson and Baur[4] associate a no less heterogeneous assemblage under the cognomen "Microsauria," we but imply the conviction herein set forth.

Concerning the phalangeal problem, the discovery that certain living Chelonia are hyperphalangeata[5]; that by Peters[6] that in the Pleurodian Pelomedusa the numerical reduction of the phalanges is in part due to fusion of more numerous elements during

[1] Sewertzoff writes (Bull. Soc. Nat. Mosc. n. s. vol. ix. 1895, p. 186): "Bei die Amphibien entspricht der Ganze Occipitalabschnitt einem einzigen Segmente, dem einfachen Occipitalbogen, so dass die Amphibien in dieser Hinsicht unter allen Cranioten, mit Ausnahme der Petromyzonten, die einfachsten Zustand zeigen." Intensely interesting in this association are the recent observations of Peter (*op. cit.* [*antea*, p. 50] pp. 590–592), based on the discovery in Ichthyophis of a postvagal nerve, having, it would seem, an essential similarity to the "spinal accessory" of the Amniota.

[2] Gadow, H.: Phil. Trans. vol. 187. 1896, p. 23.

[3] Credner, H.: Allgem. Verstell. naturwiss. Abhandlg. Berlin, Hft. xv. 1891 ("Naturwiss. Wochenschr."), pp. 1–52.

[4] *Cf.* Baur, G.: Anat. Anz. Bd. xiv. 1897, p. 148, and Bd. xi. 1896, p. 657.

[5] *Cf.* Boulenger, G. A.: Brit. Mus. Cat. Chelonians, 1889, p. 240, espec. Chitra.

[6] Peters, W.: Reise nach Mossambique, Zool. iii. Berlin, 1882, p. 6.

ontogeny; the investigation of Kükenthal, which has brought to light the remarkable fact [1] that the fourth and fifth digits of the Crocodilian fore limb are developmentally hyperphalangeate—all testify to the great potentiality of the digital blastema [2], and do away with the value of the mere numerical difference as a criterion of affinity.

The question thus resolves itself into this—are the Terrestrial Vertebrata the descendants of the afore-defined Batrachian-Reptilia or of Reptilian-Batrachia? The problem for the immediate future lies in the study of the occiput, the sternal skeleton, and the quadrate; and, to our thinking, *Sclerocephalus*, with its multisegmented and structurally simple "plastron," its "fanged" vomer, its elongated dentigerous pterygoid [3], and its quadrate, points the way.

It is certain, but most unfortunate, that in its earliest forms, the sternum, known to us only in its definitive conditions, was cartilaginous, and has been lost to us in the palæontological record. The discovery by Osborn, however, of a cartilaginous sternum in the fossil state [4], gives us hope. The decision must lie with the future. Anatomist and palæontologist must approach the question in the spirit of a combined morphological brotherhood; and its solution will mark an epoch in the progress of the vertebrate morphology of the era of its discovery.

Addendum, Nov. 16, 1900.

Shortly after the proofs of this Memoir were revised for press, there reached us a recently published paper on the organogeny of Sphenodon, by Professor H. Schauinsland, of Bremen (*Archv. Mikr. Anat.* Bd. lvi. pp. 447–867). Although it came to hand too late for comment in our pages, we observe from its perusal that it is in places erroneous, and that we should have lost nothing by its earlier appearance, since its author is insufficiently acquainted with the literature of the subject, and apparently ignorant of the recent important papers by Dendy, now more than a year old.

List of the more important Memoirs dealing with Sphenodon.

83ª. Albrecht, P. Note sur la présence d'un Rudiment de Proatlas sur un exemplaire de Hatteria punctata. *Bull. Mus. Belg.* tom. ii. pp. 185–193. (First record of pro-atlas.)

83ᵇ. ——. Epiphyses osseuses sur les Apophyses épineuses des Vertèbres d'un Reptile (Hatteria punctata, Gray). *Bruxelles*, 1883. Pp. 1–6.

86ª. Baur, G. Die zwei Centralia im Carpus von Sphenodon (Hatteria) und die Wirbel von Sphenodon und Gecko verticillatus, Laur. (G. verus, Gray). *Zool. Anz.* Bd. ix. pp. 188–190.

---

[1] Kükenthal, W.: Morphol. Jahrb. Bd. xix. 1893, p. 50.

[2] In a manner akin to that of the passing "jointing" of the hyoid cornu described in the text (*antea*, p. 48).

[3] It is unfortunate that its parasphenoid is unknown, but it must assuredly have possessed one, and that probably dentigerous.

[4] Osborn, H. F.: *op. cit. antea*, p. 14.

86[b]. Baur, G. Osteologische Notizen über Reptilien. *Zool. Anz.* Bd. ix. pp. 685–690. (*Cf.* Günther, *op. cit.* p. 746, and Baur, G., *ibid.* Bd. x. pp. 120–121.)

86[c]. ——. Osteologische Notizen über Reptilien. *Zool. Anz.* Bd. ix. pp. 733–743.

86[d]. ——. The Ribs of Sphenodon (Hatteria). *Amer. Natural.* vol. xx. pp. 979–981.

87. ——. On the Morphology of Ribs. *Amer. Natural.* vol. xxi. pp. 942–945.

88. ——. Osteologische Notizen über Reptilien. *Zool. Anz.* Bd. xii. pp. 40–47. (Parasphenoid, epipterygoid, and alisphenoid.)

89. ——. Revision meiner Mittheilungen im Zoologischen Anzeiger mit Nachträgen. *Zool. Anz.* Bd. xii. pp. 238–243. (Quadratojugale and otic bones.)

91. ——. The Lower Jaw of Sphenodon. *Amer. Natural.* vol. xxv. pp. 489–490.

95[a]. —— Ueber die Morphologie des Unterkiefers der Reptilien. *Anat. Anz.* Bd. xi. pp. 410–415.

95[b]. ——. Das Gebiss von Sphenodon (Hatteria) und einige Bemerkungen über Prof. Rud. Burckhardt's Arbeit über das Gebiss der Sauropsiden. *Anat. Anz.* Bd. xi. pp. 436–439.

84. Bayer, F. Ueber die Extremitäten einer jungen Hatteria. *Stzb. Akad. Wien,* Bd. xc. pp. 237–245.

87. Bemmelen, J. F. Beiträge z. Kenntniss d. Halsgegend b. Reptilien. I. Anat. Theil. *Bijdr. t. d. Nied. Dierkd. Ver. Amsterdam,* 1887, pp. 102–146. (Contains an accurate account of nerves, blood-vessels and glands of neck of Sphenodon.)

94. Berg, J. Zur Kenntniss der Brückenechse. *Zool. Garten,* Bd. xxxv. pp. 102–105 and pp. 146–150. (An admirable figure of Sphenodon.)

89. Boulenger, G. A. Catalogue of the Chelonians, Rhynchocephalians, and Crocodiles in the British Museum, 1889, pp. 1–3.

91. ——. On British Remains of Homœosaurus, with Remarks on the Classification of the Rhynchocephalia. *Proc. Zool. Soc.* 1891, pp. 167–172.

93. ——. On some newly-described Jurassic and Cretaceous Lizards and Rhynchocephalians. *Ann. & Mag. Nat. Hist.* (ser. 6) vol. xi. pp. 204–210.

76. Buller, W. L. Notes on the Tuatara Lizard (Sphenodon), with a Description of a supposed new Species (S. güntheri). *Trans. N. Zealand Inst.* vol. ix. pp. 317–325.

77. ——. Notice of a new Variety of Tuatara Lizard (Sphenodon) from East Cape Island. *Trans. N. Zealand Inst.* vol. x. pp. 220–221. (External characters of a live specimen described, no name given.)

78. ——. Further Notes on the Habits of the Tuatara Lizard. *Trans. N. Zealand Inst.* vol. xi. pp. 349–351. (Deals with individuals in captivity.)

98. Busch, C. H. Beiträge zur Kenntniss der Gaumenbildung bei den Reptilien. *Zool. Jahrb.* (*Anat. Abth.*) Bd. xi. pp. 441–499.

85. Colenso, W. Notes on the Bones of a Species of Sphenodon (S. diversum, Col.) apparently distinct from the Species already known. *Trans. N. Zealand Inst.* vol. xviii. 1885, pp. 118–123.

86. Cope, E. D. The Intercentrum in Sphenodon. *Amer. Natural.* vol. xx. p. 175.

88. Cornet, J. Note sur le prétendu Pro-atlas des Mammifères et de Hatteria punctata. *Bull. Ac. Belgique* (sér. 3), tom. xv. pp. 406–420.

98. Dendy, A. Summary of the principal Results obtained in a Study of the Development of the Tuatara (Sphenodon punctatus). *Proc. R. Soc.* vol. lxiii. pp. 440–443.

99[a]. ——. Outlines of the Development of the Tuatara (Sphenodon punctatus). *Quart. Journ. Micr. Sci.* vol. xlii. pp. 1–87.

99[b]. Dendy, A. On the Development of the Parietal Eye and adjacent Organs in Sphenodon. *Ibid.* pp. 111–153.

99[c]. ——. The Life-History of Tuatara (Sphenodon punctatus). *Trans. N. Zealand Inst.* vol. xxxi. pp. 249–255.

99. Dendy, A., and Howes, G. B. The Hatching of Tuatara Eggs. *Nature*, vol. lix. p. 340.

84. Dollo, L. Notes Erpétologiques. *Zool. Anz.* Bd. vii. pp. 547–548. (First description of condylar foramina of humerus. More fully described with figures in *Bull. Mus. Belg.* tom. iii. p. 151). (*Cf.* also Fürbringer, *Morph. Jahrb.* Bd. xi. pp. 484–486.)

88. ——. Sur le Proatlas. *Zool. Jahrb.* (*Anat. Abth.*) Bd. iii. pp. 433–446.

89. Fritsch, A. Fauna der Gaskohle und der Kalksteine der Permformation Böhmens, Bd. ii. Prag, 1889. (p. 58, parasphenoid; p. 52, cervical vertebræ.) (A correction in *Zool. Anz.* Bd. x. p. 115.)

88. Gadow, H. On the Modifications of the First and Second Visceral Arches, with especial reference to the Homologues of the Auditory Ossicles. *Phil. Trans.* vol. 179. pp. 451–485.

96. ——. On the Evolution of the Vertebral Column of Amphibia and Amniota. *Phil. Trans.* vol. 187, B. 1896, pp. 1–57.

98. ——. Zur Rettung von Hatteria. *Anat. Anz.* Bd. xv. pp. 41–43.

97. Goette, A. Ueber den Wirbelbau bei den Reptilien und einigen anderen Wirbelthieren. *Zeitschr. wiss. Zool.* Bd. lxii. 1897, pp. 343–394.

31. Gray, J. E. Note on a peculiar Structure in the Head of an Agama. *Zool. Miscell.* 1831, p. 13. (Genus Sphenodon.)

42. ——. Descriptions of two hitherto unrecorded Species of Reptiles from New Zealand. *Zool. Miscell.* 1842, p. 72.

69. ——. Sphenodon, Hatteria, and Rhynchocephalus. *Ann. & Mag. Nat. Hist.* (ser. 4) vol. iii. p. 167. (Gives history of three generic names.)

67. Günther, A. Contribution to the Anatomy of Hatteria (Rhynchocephalus, Owen). *Phil. Trans.* vol. 167. pp. 595–629.

90. Howes, G. B. Pro-atlas and Vomerine Teeth in Hatteria. *Proc. Zool. Soc.* 1890, pp. 357–360.

69. Huxley, T. H. On the Representatives of the Malleus and the Incus of the Mammalia in other Vertebrata. *Proc. Zool. Soc.* 1869, pp. 391–407.

98. Kallius, E. Ueber die Fovea centralis von Hatteria punctata. *Anat. Anz.* Bd. xiv. pp. 623–624. (Reply by Osawa, *ibid.* Bd. xv. pp. 226–227.)

92. Klaatsch, H. Zur Morphologie der Mesenterialbildungen am Darmkanal der Wirbelthiere. *Morphol. Jahrb.* Bd. xviii. pp. 424–433. (Detailed description for Sphenodon.)

69. Knox, F. J. On the Tuatara (Hatteria punctata, Gray), or Great Fringed Lizard of New Zealand. *Trans. N. Zealand Inst.* vol. ii. pp. 17–20.

96. Maurer, F. Die ventrale Rumpfmuskulatur einiger Reptilien. *Festschrift zum siebenzigsten Geburtstage von Carl Gegenbaur*: Leipzig, 1896. Bd. i. pp. 183–256.

77. Newman, A. K. Notes on the Physiology and Anatomy of the Tuatara (Sphenodon güntheri). *Trans. N. Zealand Inst.* vol. x. pp. 222–239. (Includes description of habits.)

96[a]. Osawa, G. Beitrag zur feineren Structur des Integumentes der Hatteria punctata. *Archv. mikr. Anat.* Bd. xlvii. pp. 570–583.

96[b]. Osawa, G. Beiträge zur Lehre von den Eingeweiden der Hatteria punctata. *Archv. mikr. Anat.* Bd. xlix. pp. 113–226.

98[a]. ——. Beiträge zur Anatomie der Hatteria punctata (Knochen, Muskeln, Nerven). *Archv. mikr. Anat.* Bd. li. pp. 481–691.

98[b]. ——. Beiträge zur Lehre von den Sinnesorganen der Hatteria punctata. *Archv. mikr. Anat.* Bd. lii. pp. 268–366.

98[c]. ——. Ueber die Stellung der Hatteria punctata in der Tierreihe. *Verhandlg. Anat. Gesellschaft,* 1898 (*Anat. Anz.* Bd. xiv., Suppl.), pp. 100–106.

98[d]. ——. Erwiederung an Gadow auf den Aufsatz "Zur Rettung von Hatteria." *Anat. Anz.* Bd. xv. pp. 289–291.

95. Perrin, A. Recherches sur les Affinités zoologiques de l'Hatteria punctata. *Ann. Sci. Nat.* (sér. 7), *Zool.* tom. xx. pp. 33–102. (Mainly deals with hind limb.)

70. Peters, H. W. Remarks on Exhibition of a Specimen of Sphenodon. *Stzb. Ges. naturf. Fr. Berlin,* 1870, p. 54.

74. ——. Ueber die Gehörknöchelchen und ihr Verhältniss zu dem ersten Zungenbeinbogen bei Sphenodon punctatus. *Monatsber. Ak. Wiss. Berlin,* 1874, pp. 40–45.

81. Reischek, A. Notes on Zoological Researches made on the Chicken Islands, east coast of the North Island, N.Z. *Trans. N. Zealand Inst.* vol. xiv. pp. 274–277. (Original description of supposed commensal habit.)

90. Röse, C. Beiträge zur vergleichenden Anatomie des Herzens der Wirbelthiere. *Morphol. Jahrb.* Bd. xvi. pp. 27–96. (Deals with sinus venosus in detail.)

96. Ruge, G. Ueber das Peripherische Gebiet des Nervus facialis bei Wirbelthieren. *Festschrift zum siebenzigsten Geburstage von Carl Gegenbaur* : Leipzig, 1896. Bd. iii. pp. 195–348.

98[a]. Schauinsland, H. Zur Entwickelung von Hatteria. *Stzb. Ak. Berlin,* 1898, pp. 629–631. (Preliminary account on general development, based on material obtained in Cook's Island, Dec. 1896 to Jan. 1897.)

98[b]. ——. Beiträge zur Biologie der Hatteria. *Ibid.* pp. 701–704. (Breeding-habits and general development.)

98[c]. ——. Beiträge zur Biologie u. Entwickelung der Hatteria, nebst Bemerkungen u. d. Entwickelung der Sauropsiden. *Anat. Anz.* Bd. xv. pp. 309–334.

93. Siebenrock, F. Zur Osteologie des Hatteria-Kopfes. *Stzb. Akad. Wien,* Bd. cii. Abth. i. pp. 250–268. (English translation in *Ann. & Mag. Nat. Hist.* (ser. 6) vol. xiii. pp. 297–311.)

99. Thilenius, G. Vorläufiger Bericht über die Eiablage und erste Entwickelung der Hatteria punctata. *Stzb. Akad. Berlin,* Bd. xiv. pp. 247–256. (Apropos of investigations conducted during 1898–1899 at Te Karewa, St. Stephen's Island, N.Z.)

90. Thomas, A. P. W. Preliminary Note on the Development of the Tuatara (Sphenodon punctatum). *Proc. R. Soc. London,* vol. xlviii. pp. 152–156. (Records sexual differences and gives a description of the egg.)

82. Ward. "The Hatteria (Sphenodon) punctatus." *Nat. Sci. Bull.* vol. i. 1882, pp. 14–15. (Mainly a popular account of an expedition to obtain the living animal.) (French translation by Bonnier in *Bull. Sci. Dép. Nord,* tom. xix. pp. 89–97.)

93. Werner, F. Beobachtungen an Sphenodon (Hatteria) punctatus. *Zool. Garten,* Bd. xxxiv. pp. 335–339. (Observations on an adult in captivity.)

PLATE I.

EXPLANATION OF THE PLATES[1].

PLATE I

SPHENODON PUNCTATUS.—VERTEBRAL COLUMN AND RIBS.

a., arch of the atlas; *a.*, body of atlas (odontoid peg); *c.c.*, caudal canal; *c.v.*, cartilaginous vertebra; *f.t.*, fibrous tissue; *h.a.*, accessory hypapophysis; *i.p.*, primary intercentrum; *i.p.'*, median intercentrum; *i.p.''*, chevron-bone; *i.s.*, secondary intercentrum; *i.sg.*, interseptal segment; *my.*, myelon (spinal cord); *n.a.*, neural arch; *nc.*, notochord; *nc.e.*, chordal epithelium; *nc.s.*, chordal sheath; *n.p.*, intravertebral chordal plate; *n.p.'*, intervertebral chordal plate; *n.sp.*, neural spine; *oc.c.*, occipital condyle; *o.v.*, osseous vertebra; *r.cd.*, caudal rib; *r.s.*, sacral rib; *r.t.*, trunk rib; *s.l.*, splitting lamina; *s.o.*, skeletogenous sheath; *t.a.*, interarticular tissue; *v.c.*, vesicula centralis.

Fig. 1. *Stage P. Vertebral Column*:—Lateral longitudinal section at about the region of vertebræ 6–8. × 50.

Fig. 2. *Stage P. The same*:—Median longitudinal section through the region of fig. 1. × 50.

Fig. 3. *Stage P. The same*:—Transverse section through the intervertebral region of caudal segments 2–3. × 40.

Fig. 4. *Stage P. The same*:—Section through a vertebral region—the 6th segment in front of fig. 3. × 40.

Fig. 5. *Stage Q. Vertebral Column*:—Lateral longitudinal section in the region of vertebræ 20–23. × 40.

Fig. 6. *Stage Q. The same*:—Median longitudinal section through vertebræ 20–23. × 40.

Fig. 7. *Stage Q. The same*:—Longitudinal section (slightly oblique) through caudal vertebræ 3–6. × 40.

Fig. 8. *Stage Q. The same*:—Median longitudinal section through the basi-occipital and the four anterior cervical vertebræ. × 40.

Fig. 9. *Stage S. Vertebral Column*:—Longitudinal section through the basi-occipital and the three anterior cervical vertebræ. × 25.

Fig. 10. *Stage S. The same*:—Median longitudinal section through vertebræ 13–15. × 25.

Fig. 11. *Stage S. The same*:—Transverse section through the intervertebral region 5–6. × 25.

Fig. 12. *Stage S. The same*:—Ventral aspect of the last presacral to the 9th caudal vertebræ showing free caudal ribs. × 5.

Fig. 13. *Stage T. Vertebral Column*:—Median longitudinal section through vertebræ 7–10. × 18.

Fig. 14. *Stage T. The same*:—Median longitudinal section through intercentrum 8–9 of fig. 13, showing minute structure. × 50.

Fig. 15. *Adult. Vertebral Column*:—Median longitudinal section through vertebræ 9–11. × 11.

Fig. 16. *Adult. The same*:—Ventral aspect of the 10th to the 20th vertebræ showing an abnormal condition of the intercentra. ¾ nat. size.

Fig. 17. *Adult. The same*:—Median longitudinal section at about the region of the 12th caudal vertebra. × 5.

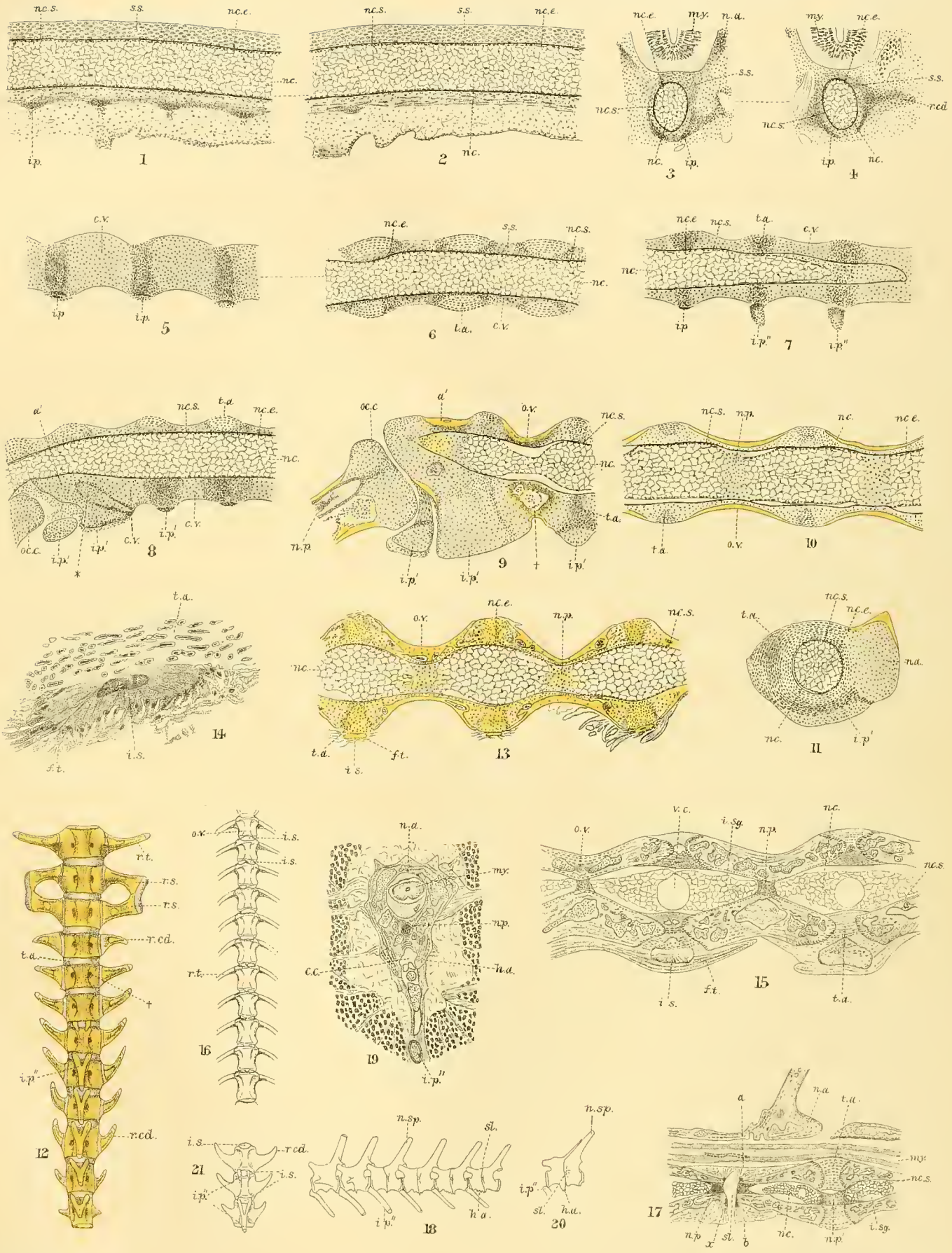
Fig. 18. *Adult. The same*:—Caudal vertebræ 7–12 from the left side. ¾ nat. size.

Fig. 19. *Adult. The same*:—Transverse section through plane *a–b* of fig. 17. × 11.

Fig. 20. *Adult. The same*:—Caudal vertebra 11 from the left side. ¾ nat. size.

Fig. 21. *Adult. The same*:—Caudal vertebræ. ¾ nat. size.

[1] In all the Plates, where colouring has been employed, blue indicates hyaline cartilage and yellow bone, with the exception of Pl. I. fig. 13.



H.H.S. del.
M.P. Parker lith.

Geo West & Sons imp

SPHENODON PUNCTATUS.

Vertebral Column & Ribs.

PLATE II.

PLATE II.

SPHENODON PUNCTATUS.—VERTEBRAL COLUMN AND RIBS, GASTRALIA, AND TEETH.

a., arch of atlas; *ab.'*, abdominal rib, median portion; *ab.''*, abdominal rib, lateral portion; *c.au.*, auditory capsule; *d.*, dentary; *e.o.*, exoccipital; *g.t.*, gastralia tissue tracts; *i.p.'*, median intercentrum; *i.p.''*, chevron-bone; *m.*, costo-cervical muscle; *m.'*, ligament of costo-cervical muscle; *mk.*, Meckel's cartilage; *mx.*, maxilla; *my.*, myelon (spinal cord); *n.'*, first spinal nerve; *n.xii.*, twelfth cranial nerve; *n.a.*, neural arch; *nc.*, notochord; *nc.e.*, chordal epithelium; *nc.s.*, chordal sheath; *n.p.*, intravertebral chordal plate; *n.s.*, neurocentral suture; *o.v.*, osseous vertebra; *p.a.*, pro-atlas; *px.*, premaxilla; *r.c.*, cervical rib; *r.cd.*, caudal rib; *r.s.*, sacral rib; *r.t.*, trunk rib; *t.a.*, interarticular tissue; *t.ch.*, cheek-tooth; *t.d.*, developing tooth; *t.f.*, fully-formed tooth (fused with bone); *t.i.*, inner incisor; *t.m.*, middle incisor; *t.o.*, outer incisor; *t.p.*, transpalatine; *u.p.*, uncinate process.

Fig. 1. *Stage S. Anterior cervical vertebræ* :—The first five vertebræ showing anterior cervical ribs, lateral aspect. × 8.

Fig. 2. *Stage T. The same* :—The first 5–6 vertebræ showing osseous and so-called ligamentous cervical ribs from left side, ventro-lateral aspect. × 4.

Fig. 3. *Stage S. The "Pro-Atlas"* :—Lateral longitudinal section, including the exoccipital. × 20.

Fig. 4. *Stage S. The Ribs* :—Transverse section of last presacral vertebral segment. × 20.

Fig. 5. *Stage S. The same* :—Transverse section of the second sacral vertebral segment. × 20.

Fig. 6. *Stage S. The same* :—Transverse section of the fourth caudal vertebral segment. × 20.

Fig. 7. *Stage R. Uncinate process* :—Section through a poststernal rib showing development of uncinate process. × 25.

Fig. 8. *Stage S. Abdominal ribs* :—Ventral aspect of ribs 3–5. × 8.

Fig. 9. *Stage S. The same* :—Ventral aspect of ribs 16–18 of right side. × 11.

Fig. 10. *Stage T. The same* :—Ventral aspect of ribs 7–16 showing irregular union of parts. × 2.

Fig. 11. *Stage R. Notochordal plate* :—Transverse section showing first origin. × 40.

Fig. 12. *Stage S. The same* :—Transverse section at full formation. × 25.

Fig. 13. *Stage S. Chevron-bones* :—Transverse section showing attachment to fourth caudal vertebra. × 25.

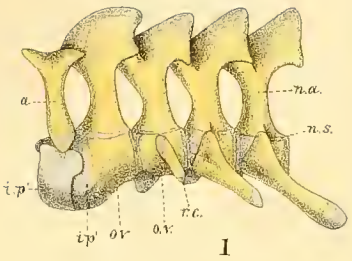
Fig. 14. *Stage S. Incisor teeth* :—Front aspect. × 5.

Fig. 15. *Stage T. The same* :—Front aspect. × 4.

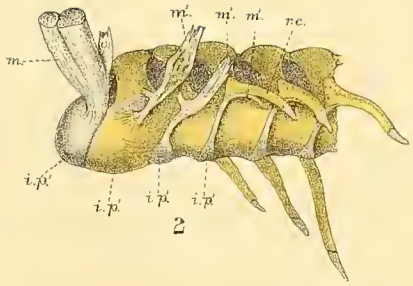
Fig. 16. *Stage T. The same* :—Median longitudinal section through second upper incisor and associated parts. × 23.

Fig. 17. *Stage T. Maxillo-palatine teeth* :—Combined drawing—the teeth already confluent with the bone being indicated in outline, the developing teeth in colour. × 13.

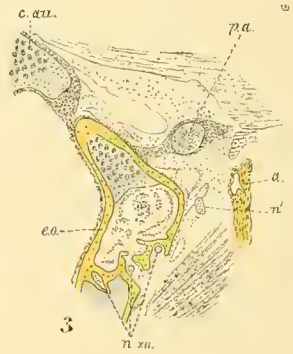
Fig. 18. *Stage S. Cheek-tooth* :—Transverse section, including dentary and Meckel's cartilage. × 20.



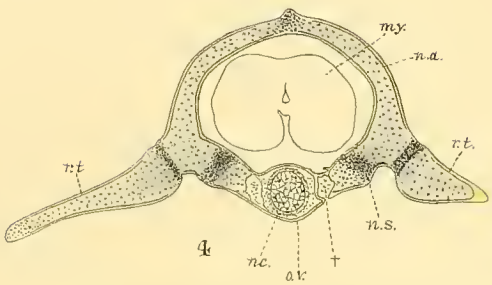
1



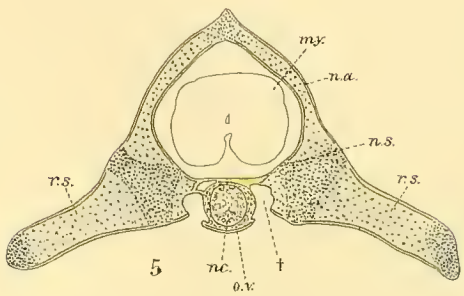
2



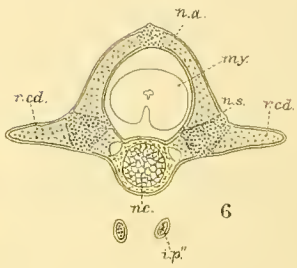
3



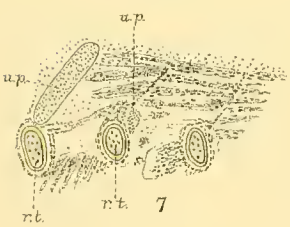
4



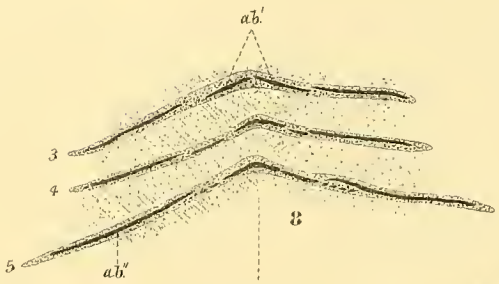
5



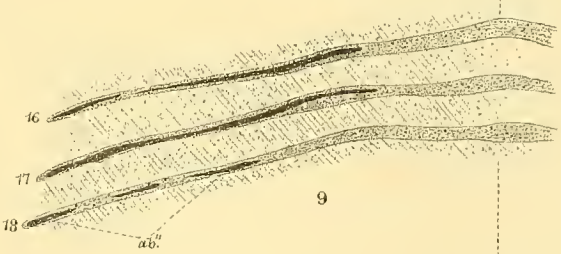
6



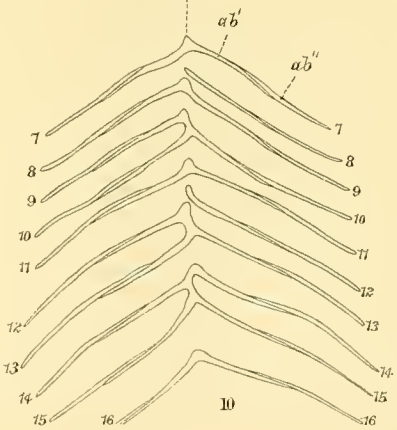
7



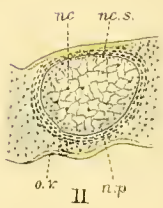
8



9

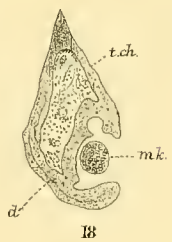


10

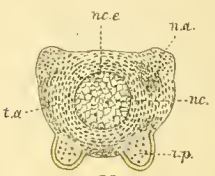


11

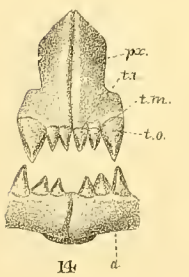
12



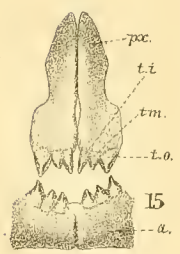
13



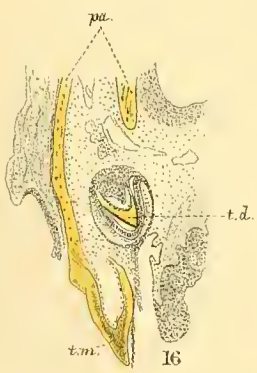
13



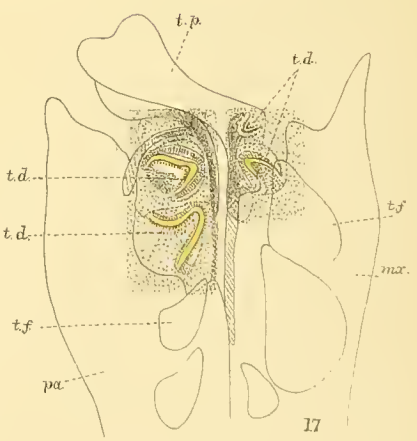
14



15



16



17

H. H. S. del.
M. P. Parker lith

Geo West & Sons imp

SPHENODON PUNCTATUS.

Vertebral Column & Ribs, Gastralia & Teeth.

PLATE III.

PLATE III.

SPHENODON PUNCTATUS.—DEVELOPING SKULL, EARLIER STAGES.

The figures on this Plate are of wax models reconstructed from microscopic sections, the skeletal parts being alone represented. The fenestræ and interspaces in the chondrocranium are for the most part occupied by membrane (not indicated), except in so far as they transmit nerves and blood-vessels (*cf.* Pl. IV. fig. 10).

---

an., angular; *ar.*, articular; *b.s.'*, basipterygoid process; *c.'*, anterior semicircular canal; *c.au.*, auditory capsule; *c.r.*, coronoid; *d.*, dentary; *e.c.*, extrastapedial cartilage; *e.n.*, external nares; *e.o.*, exoccipital; *epg.*, epipterygoid; *e.s.*, ethmosphenoidal plate; *ex.*, extranasal; *ex.*$^{1-4}$, extranasal processes; *f. i.–xii.*, foramina for exit of cranial nerves; *f.a.*, foramen for ophthalmic branch of the carotid; *f.e.*, ethmoidal foramen; *f.i.*, interorbital fenestra; *f.j.*, foramen for jugular vein; *f.m.*, foramen magnum; *f.n.*, lateral cranial fenestra; *fr.*, frontal; *h.*, hyoid; *h.'*, anterior cornu of the hyoid; *h.''*, posterior cornu of the hyoid; *i.n.*, internal nares; *j.*, jugal; *mk.*, Meckel's cartilage; *mx.*, maxilla; *mx.'*, maxillary process; *n.a.p.*, alinasal process; *nc.*, notochord; *n.c.*, nasal capsule; *n.c.'*, supranasal process; *n.c.''*, prenasal process; *n.f.'*, nasal fenestra; *n.pa.p.*, naso-palatine process; *n.p.p.*, naso-premaxillary process; *ns.*, nasal; *n.v.p.*, inferior naso-vomerine process; *oc.c.*, occipital condyle; *os.*, otosphenoidal plate; *os.*$^{1-5}$, otosphenoidal processes; *p.*, parietal; *pa.*, palatine; *par.*, parachordal; *p.f.*, prefrontal; *pg.*, pterygoid; *pg.'*, pterygoid process; *p.o.*, postorbital; *po.f.*, postfrontal; *p.p.*, parotic process; *p.q.*, pterygo-quadrate: *ps.*, presphenoidal cartilage; *p.s.*, parasphenoid; *px.*, premaxilla; *py.'*, pituitary foramen; *q.*, quadrate; *q.'*, otic process of quadrate; *q.j.*, quadrato-jugal; *s.a.*, supra-angular; *sb.*, subnasal; *s.i.*, interorbital septum; *s.mx.*, septo-maxillary; *s.o.'*, supraoccipital cartilage; *sp.*, splenial; *sq.*, squamosal; *sq.''*, posterior process of squamosal; *s.st.*, suprastapedial cartilage; *st.*, stapes; *t.p.*, transpalatine; *tr.*, trabecula; *vo.*, vomer.

Fig. 1[1]. *Stage P. Developing chondrocranium*:—Left lateral aspect. The arrow indicates the direction of the longitudinal axis of the embryo as it lay coiled. × 13.

Fig. 2[1]. *Stage P. The same*:—Ethmoidal, trabecular, and sphenoidal regions, dorsal aspect. × 13.

Fig. 3[1]. *Stage P. The same*:—Parachordal and auditory regions, dorsal aspect. × 13.

Fig. 4. *Stage Q. Developing chondrocranium*:—Lateral aspect. × 8.

Fig. 5. *Stage Q. Developing skull*:—Lateral aspect. × 8.

Fig. 6. *Stage Q. Developing chondrocranium*:—Ventral aspect. × 8.

Fig. 7. *Stage Q. The same*:—Dorsal aspect. × 8.

Fig. 8. *Stage R. Developing chondrocranium*:—Lateral aspect. × 8.

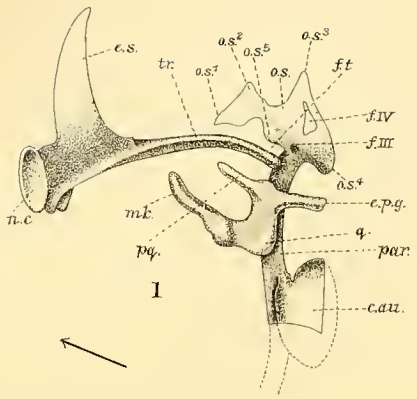
Fig. 9. *Stage R. Developing skull*:—Posterior aspect. × 8.

Fig. 10. *Stage R. The same*:—Lateral aspect. × 8.

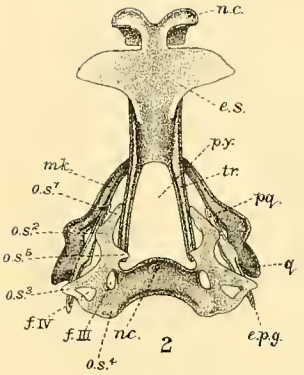
Fig. 11. *Stage R. The same*:—Dorsal aspect. × 8.

Fig. 12. *Stage R. The same*:—Ventral aspect. × 8.

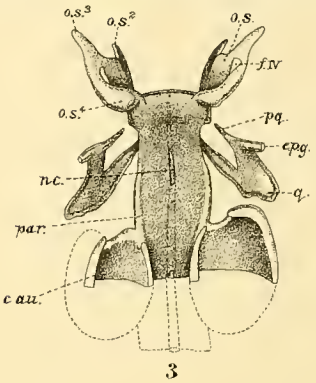
[1] In these figures the uncoloured areas represent pro-cartilage.



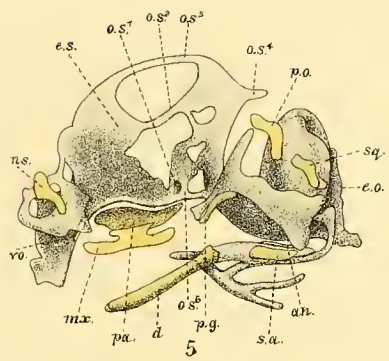
1



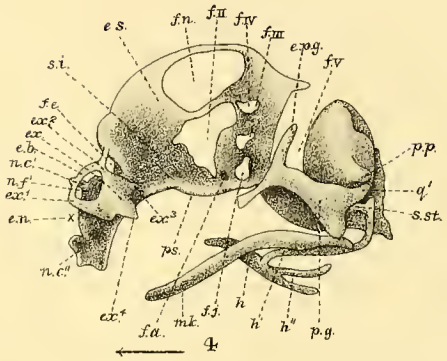
2



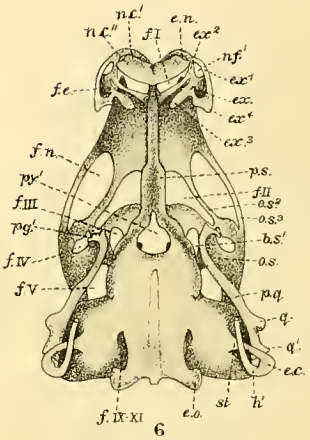
3



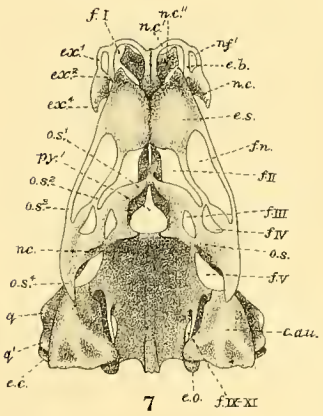
5



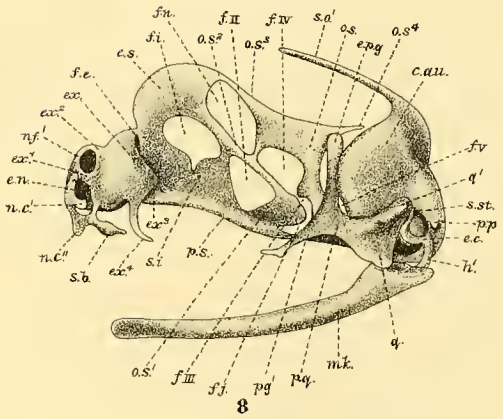
4



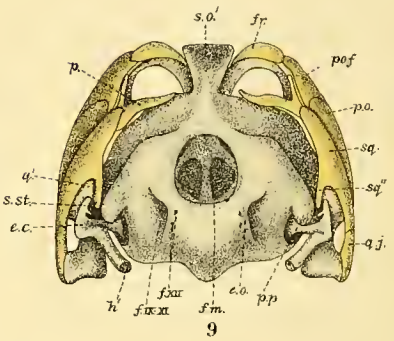
6



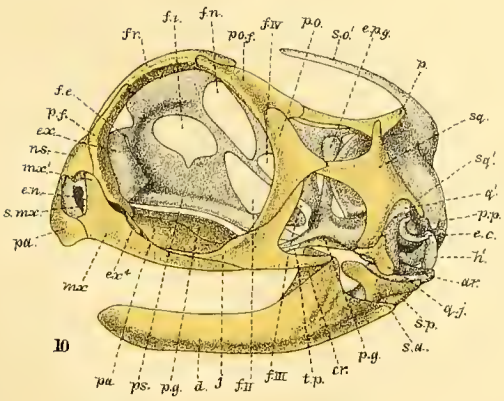
7



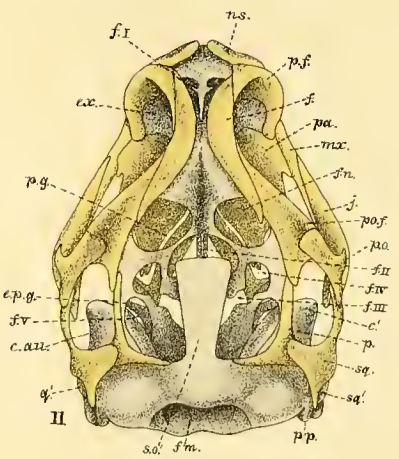
8



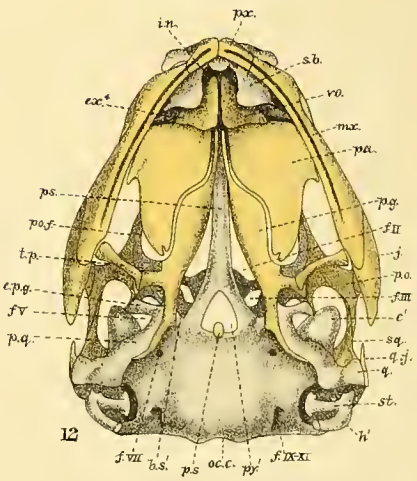
9



10



11



12

H.H.S del
M.P, Parker lith.

Geo. West & Sons imp.

SPHENODON PUNCTATUS.

Developing skull, earlier stages.

PLATE IV.

PLATE IV.

SPHENODON PUNCTATUS.—DEVELOPING SKULL, LATER STAGES.

an., angular; *ar.*, articular; *b.o.*, basi-occipital; *b.s.*, basisphenoid; *b.s.'*, basipterygoid process; *c.'*, anterior semicircular canal; *c.''*, posterior semicircular canal; *cr.*, coronoid; *d.*, dentary; *e.c.*, extrastapedial cartilage; *e.n.*, external nares; *e.o.*, exoccipital; *e.p.g.*, epipterygoid; *e.s.*, ethmosphenoidal plate; *ex.*, extranasal; *ex.*^{1}–*ex.*^{5}, extranasal processes; *f. i.–xii.*, foramina for exit of cranial nerves *f.*, fenestra in the suprastapedial cartilage; *f.e.*, ethmoidal foramen; *f.i.*, interorbital fenestra; *f.j.*, foramen for jugular vein; *f.n.*, fenestra in the anterior wall of the brain-case; *f.p.*, parietal foramen; *fr.*, frontal; *h.'*, anterior cornu of the hyoid; *i.n.*, internal nares; *j.*, jugal; *l.d.*, lachrymal duct; *mk.*, Meckel's cartilage; *mp.*, meniscus pterygoideus; *mx.*, maxilla; *mx.'*, maxillary process; *n. v.*, *vi.*, cranial nerves; *n.c.*, nasal capsule; *n.c.'*, supra-nasal process; *n.c.''*, prenasal process; *nf.'*, *nf.''*, nasal fenestræ; *ns.*, nasal; *oc.c.*, occipital condyle; *op.*, opisthotic; *o.s.*, otosphenoidal plate; *o.s.*$^{1-5}$, otosphenoidal processes; *p.*, parietal; *pa.*, palatine; *p.f.*, prefrontal; *p.g.*, pterygoid; *p.g.'*, pterygoid process; *p.o.*, postorbital; *po.f.*, postfrontal; *p.p.*, parotic process; *pro.*, prootic; *ps.*, presphenoidal cartilage; *p.s.*, parasphenoid; *px.*, premaxilla; *py.*, pituitary body; *q.*, quadrate; *q.'*, otic process of quadrate; *q.j.*, quadrato-jugal; *s.a.*, supra-angular; *sb.*, subnasal; *s.i.*, interorbital septum; *s.mx.*, septo-maxillary; *s.o.*, supra-occipital; *s.o.'*, supra-occipital cartilage; *sp.*, splenial; *sq.*, squamosal; *sq.'*, anterior process of squamosal; *sq.''*, posterior process of squamosal: *s.st.*, suprastapedial cartilage; *st.*, stapes; *t.p.*, trans-palatine; *vo.*, vomer.

Fig. 1. *Stage R–S. The head* :—Transverse section through epipterygoid region (γ–δ of fig. 4). × 6.

Fig. 2. *Stage R–S. The same* :—Combined figure of two transverse sections through the nasal region (α–β of fig. 4), the left half several sections in front of the right. × 15.

Fig. 3. *Stage R–S. The same* :—Transverse sections showing detailed relations of pterygoid and basisphenoid (seven sections in front of fig. 1). × 18.

Fig. 4. *Stage S. Developing skull* :—Lateral aspect. × 5.

Fig. 5. *Stage S. The same* :—Dorsal aspect. × 5.

Fig. 6. *Stage S. The same* :—Ventral aspect. × 5.

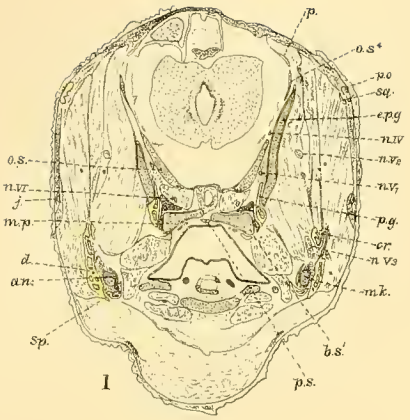
Fig. 7. *Stage S. The same* :—Posterior aspect. × 5.

Fig. 8. *Stage T. Developing skull* :—Dorsal aspect. × 3.

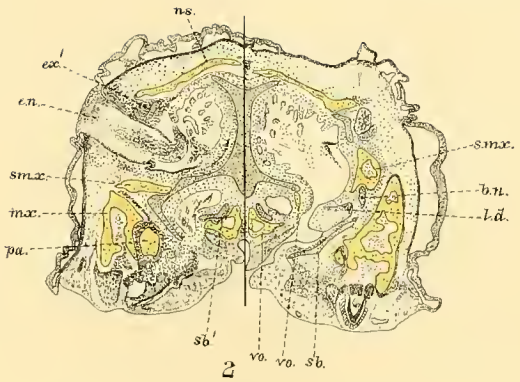
Fig. 9. *Stage T. The same* :—Posterior aspect. × 3.

Fig. 10. *Stage T. The chondrocranium* :—With endostoses and the parasphenoid; as seen after removal of the mandibular skeletal arch. Left lateral aspect. × 3.

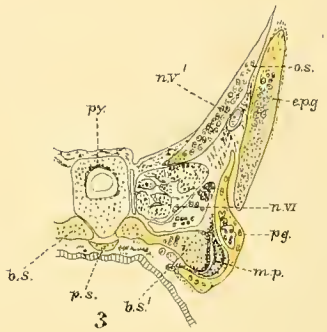
Fig. 11. *Stage T. The left pterygo-quadrate arch and squamosal* :—Lateral aspect. × 5.



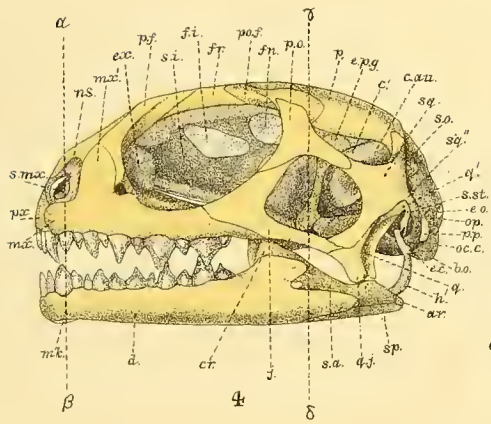
1

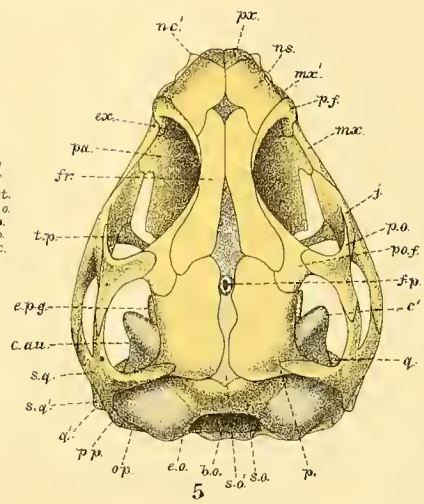


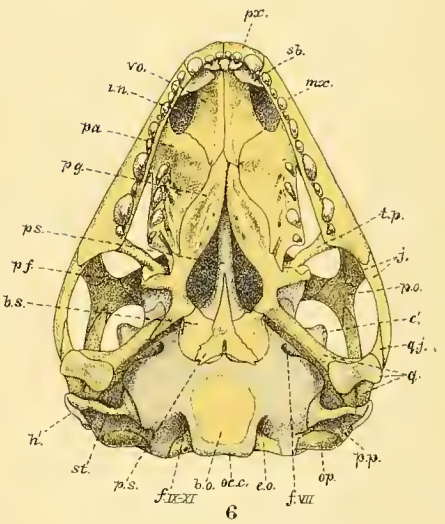
2

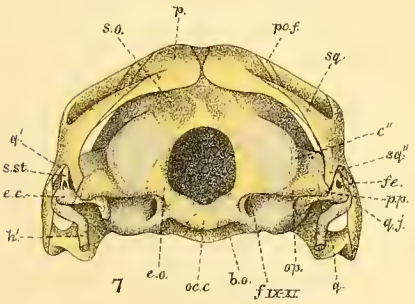


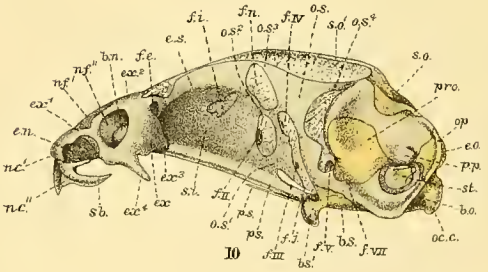
3

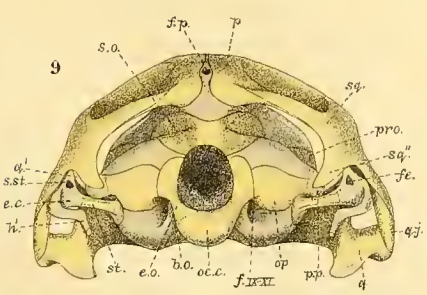


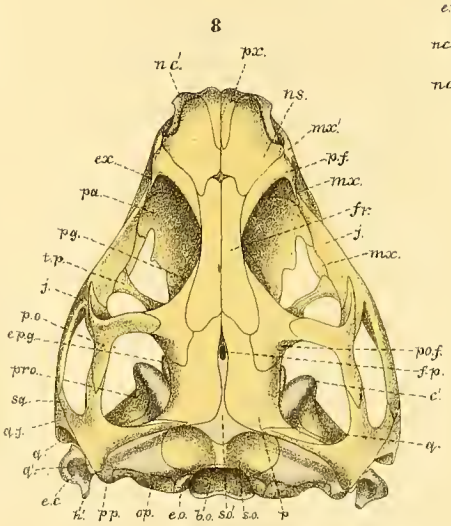


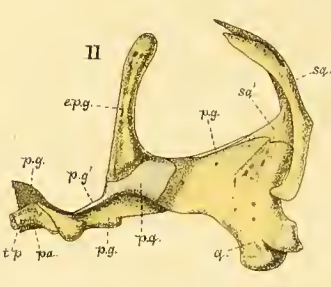












H H. S. del.
M. P. Parker lith.

Geo. West & Sons imp.

SPHENODON PUNCTATUS.

Developing skull, later stages.

PLATE V.

PLATE V.

SPHENODON PUNCTATUS.—THE QUADRATE, HYOID, AND COLUMELLA AURIS.

an., angular; *b.*, boundary between stapes and extrastapedial cartilage; *b.a.*, branchial arch; *b.c.*, branchial cleft; *c.'''*, horizontal semicircular canal; *ca.*, carotid artery; *ca.'*, branch of carotid artery; *c.au.*, auditory capsule; *e.c.*, extrastapedial cartilage; *eu.*, eustachian recess; *fe.*, fenestra in suprastapedial cartilage; *h.'*, anterior cornu of the hyoid; *j.v.*, jugular vein; *mk.*, Meckel's cartilage; *mt.*, mouth; *n. v.–xi.*, cranial nerves; *n. vii.'*, branch of chorda tympani; *ph.*, pharynx; *p.p.*, parotic process; *pq.*, pterygoquadrate; *q.*, quadrate; *q.'*, otic process of quadrate; *s.a.*, supra-angular; *sq.'*, anterior process of squamosal; *sq.''*, posterior process of squamosal; *s.st.*, supra-stapedial cartilage; *st.*, columella (stapes); *st.'*, boundary between columella and extrastapedial cartilage.

Figs. 1–5. *Stage P.* A series of sections, in order from within outwards, showing the primary relationships of the columella auris to the hyoid and quadrate. × 40.

Fig. 1. Represents the most internal section No. 1.
Fig. 2. Represents section No. 6.
Fig. 3. „ „ No. 8.
Fig. 4. „ „ No. 19.
Fig. 5. „ „ No. 27.

Fig. 6–11. *Stage Q.* A similar series to the above. × 25.

Fig. 6. Represents the most internal section No. 1.
Fig. 7. Represents section No. 11.
Fig. 8. „ „ No. 26.
Fig. 9. „ „ No. 36.
Fig. 10. „ „ No. 46.
Fig. 11. „ „ No. 57.

Fig. 12. *Stage R.* Transverse section of auditory region passing through quadrate and columella auris. × 25.

Figs. 13–14. *Stage S.* Sections, in the same order as figs. 1–5, showing the relation of the suprastapedial cartilage to the quadrate. × 20.

Fig. 13. Represents the more internal section No. 1.
Fig. 14. Represents section No. 16.

H.H.S. del.
M.P. Parker lith

Geo. West & Sons imp

SPHENODON PUNCTATUS.

The Quadrate, Hyoid, & Columella auris

PLATE VI.

PLATE VI.

SPHENODON PUNCTATUS.—CRANIO-FACIAL MEMBRANE-BONES AND APPENDICULAR SKELETON.

ac., acetabulum; *an.*, angular; *c.*, centrale; *c.i.p.*, ischio-pubic cartilage; *cl.*, clavicle; *cor.*, coracoid; *cor.'*, sulcus coracoideus; *cor.''*, foramen for supracoracoideus nerve; *d.*, dentary; *e.*, epipubis; *ep.*, epiphysis; *F.*, fibula; *f.*, fibulare; *f.b.*, foramen for arteria perforans mesopodii; *f.c.*, foramen cordiforme; *f.ec.*, ectepicondylar foramen; *f.en.*, entepicondylar foramen; *f.o.*, obturator foramen; *fr.*, frontal; *g.f.*, glenoid fossa; *hp.*, hypoischium; *i.*, intermedium; *i.c.*, interclavicle; *il.*, ilium; *is.*, ischium; *j.*, jugal; *l.i.p.*, ischio-pubic ligament (ligamentum medianum pelvis); *m.i.*, metischial process; *mn.*, meniscus tarsale; *mx.*, maxilla; *mx.'*, maxillary process; *ns.*, nasal; *p.*, parietal; *pa.*, palatine; *pb.*, pubis; *pb.'*, prepubic process; *p.f.*, prefrontal; *pg.*, pterygoid; *pi.*, pisiform; *p.o.*, postorbital; *po.c.*, postaxial centrale; *po.f.*, postfrontal; *pr.c.*, preaxial centrale; *pro.t.*, proximal tarsal; *px.*, premaxilla; *q.j.*, quadrato-jugal; *R.*, radius; *rd.*, radiale; *r.t.*, trunk rib; *s.*, sternum; *s.a.*, supra-angular; *sc.*, scapula; *sc.'*, acromial process; *sc.''*, suprascapula; *se.*, sesamoid; *s.mx.*, septo-maxillary; *s.n.*, poststernal notch; *sp.*, splenial; *sq.*, squamosal; *sq.''*, posterior process of squamosal; *T.*, tibia; *t.*, tibiale; *t.c.*, tarsal centrale; *t.p.*, transpalatine; *U.*, ulna; *u.*, ulnare; *vo.*, vomer; I.–V., metacarpals and metatarsals; 1–5, carpals and tarsals.

Fig. 1. *Stage S. The membrane-bones* :—Bones from roof of skull and side of head. × 5

Fig. 2. *Stage S. The same* :—Bones from roof of mouth. × 5.

Fig. 3. *Stage S. The same* :—Bones from lower jaw. × 5.

Fig. 4. *Stage Q. Pectoral girdle and sternum* :—Longitudinal section with developing clavicle. × 25.

Fig. 5. *Stage R. Pectoral girdle and sternum* :—Ventral aspect. × 8.

Fig. 6. *Stage T. Pectoral girdle and sternum* :—Ventral aspect. × 2.

Fig. 7. *Stage Q. Pelvic girdle* :—Ventral aspect (from wax model). × 8.

Fig. 8. *Stage R. Pelvic girdle* :—Ventral aspect. × 5.

Fig. 9. *Stage T. Pelvic girdle* :—Ventral aspect. × 2.

Fig. 10. *Stage Q. Humerus* :—Distal end, ventral aspect (from wax model). × 15.

Fig. 11. *Stage Q. Right carpus* :—Horizontal section. × 20.

Fig. 12. *Stage T. Right carpus* :—Dorsal aspect, showing normal condition of centralia. × 4.

Fig. 13. *Stage T. Left carpus* :—Dorsal aspect, showing abnormal condition of centralia from same animal as fig. 10. × 4.

Fig. 14. *Small Adult. Right carpus* :—Dorsal aspect. × 2.

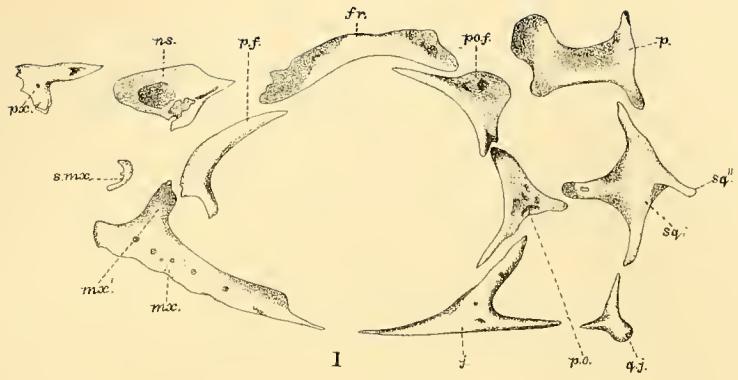
Fig. 15. *Stage Q. Left tarsus* :—Early period, horizontal section. × 20.

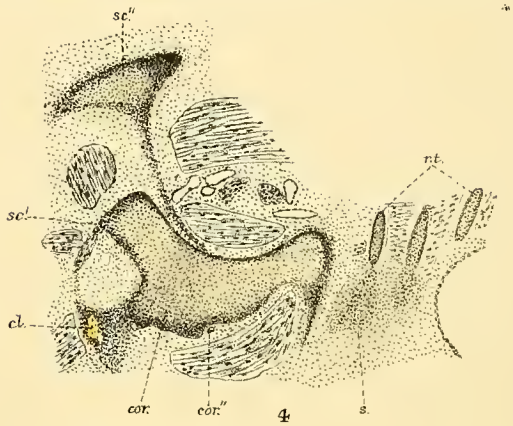
Fig. 16. *Stage Q. Right carpus* :—Late period, horizontal section. × 20.

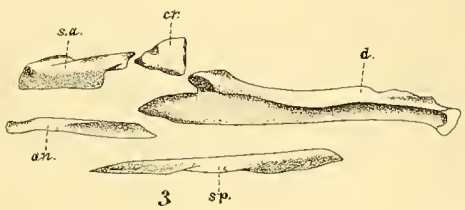
Fig. 17. *Stage R. Left tarsus* :—Horizontal section. × 15.

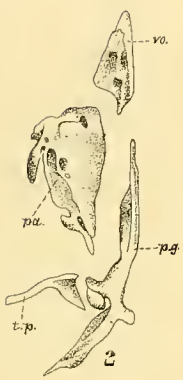
Fig. 18. *Adult. Right tarsus* :—Dorsal aspect. × 2.

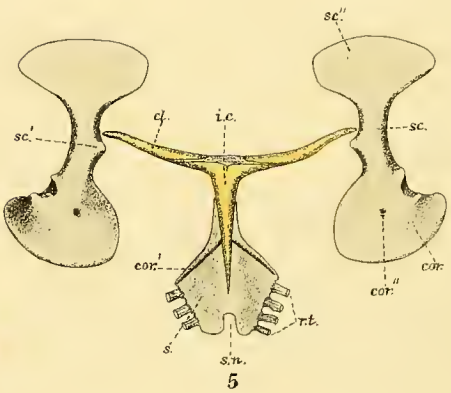
Fig. 19. *Adult. Portion of left tarsus* :—Dorsal aspect, showing ulnar sesamoid. × 2.

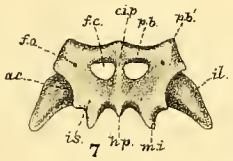


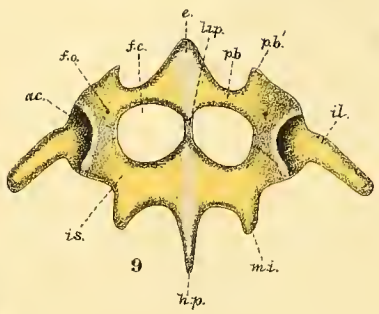


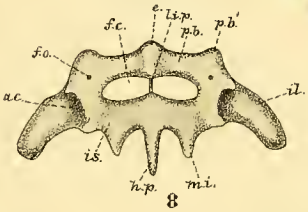


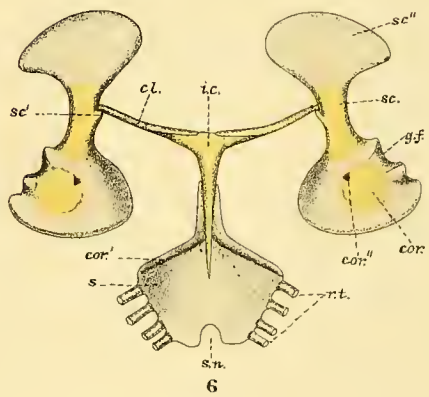


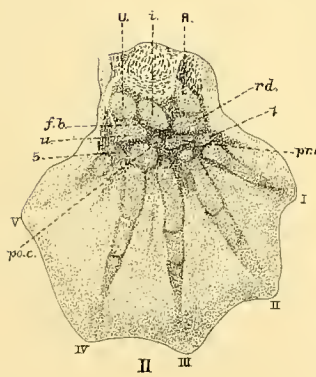


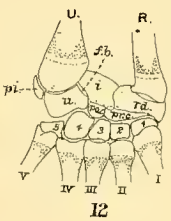


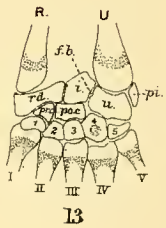


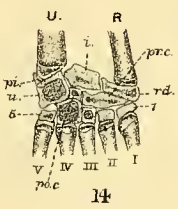


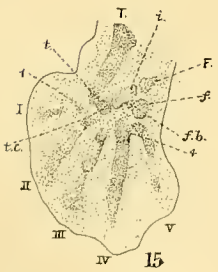


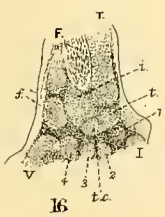


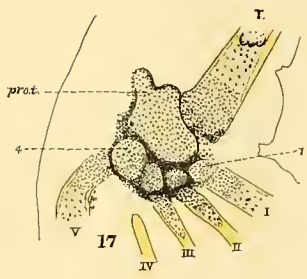


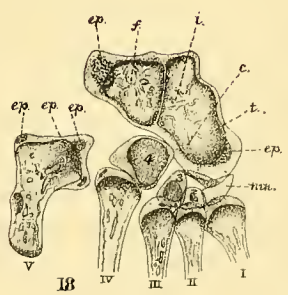


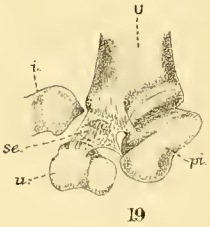












H.H.S. del.
M.P. Parker lith.

Geo West & Sons imp

SPHENODON PUNCTATUS.

Cranio-facial membrane bones, & Appendicular Skeleton.

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON
(continued).

	To Fellows. £ s. d.	To the Public. £ s. d.
VOLUME XIII. (1891–1895, containing 62 Plates) . . Price	6 8 3	8 11 0
Part 1. (1891, containing 6 Plates) . . . . . „	0 15 9	1 1 0
„ 2. (1891, containing 6 Plates) . . . . . „	0 15 9	1 1 0
„ 3. (1891, containing 6 Plates) . . . . . „	0 18 0	1 4 0
„ 4. (1892, containing 1 Plate) . . . . . „	0 4 6	0 6 0
„ 5. (1893, containing 9 Plates) . . . . . „	0 11 3	0 15 0
„ 6. (1893, containing 4 Plates) . . . . . „	0 9 0	0 12 0
„ 7. (1893, containing 6 Plates) . . . . . „	0 9 0	0 12 0
„ 8. (1894, containing 6 Plates) . . . . . „	0 9 0	0 12 0
„ 9. (1894, containing 6 Plates) . . . . . „	0 11 3	0 15 0
„ 10. (1895, containing 5 Plates) . . . . . „	0 9 0	0 12 0
„ 11. (1895, containing 7 Plates and Title and Index) „	0 15 9	1 1 0
VOLUME XIV. (1896–1898, containing 47 Plates) . Price	5 5 0	7 0 0
Part 1. (1896, containing 2 Plates) . . . . . „	0 6 0	0 8 0
„ 2. (1896, containing 6 Plates) . . . . . „	0 9 0	0 12 0
„ 3. (1897, containing 9 Plates) . . . . . „	0 15 9	1 1 0
„ 4. (1897, containing 10 Plates) . . . . . „	1 10 0	2 0 0
„ 5. (1898, containing 2 Plates) . . . . . „	0 6 0	0 8 0
„ 6. (1898, containing 7 Plates) . . . . . „	0 18 0	1 4 0
„ 7. (1898, containing 6 Plates) . . . . . „	0 11 3	0 15 0
„ 8. (1898, containing 5 Plates and Title and Index) „	0 9 0	0 12 0
VOLUME XV.		
Part 1. (1898, containing 8 Plates) . . . . . Price	0 15 9	1 1 0
„ 2. (1899, containing 5 Plates) . . . . . „	0 9 0	0 12 0
„ 3. (1899, containing 4 Plates) . . . . . „	0 9 0	0 12 0
„ 4. (1899, containing 4 Plates) . . . . . „	0 9 0	0 12 0
„ 5. (1900, containing 24 Plates) . . . . . „	2 12 6	3 10 0
VOLUME XVI.		
Part 1. (1901, containing 6 Plates) . . . . . Price	0 18 0	1 4 0

CONTENTS.

I. *On the Development of the Skeleton of the Tuatara*, Sphenodon punctatus; *with Remarks on the Egg, on the Hatching, and on the Hatched Young. By* G. B. Howes, *LL.D., F.R.S., and* H. H. Swinnerton, *B.Sc., Marshall Scholar, R. Coll. Sci. Lond.* (*From the Huxley Research Laboratory.*) (Plates I.–VI.) . . . . . page 1

THE PUBLICATIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

The scientific publications of the Zoological Society of London are of two kinds—"Proceedings," published in an octavo form, and "Transactions," in quarto.

According to the present arrangements, the "Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the "Proceedings" by the Committee of Publication. A large number of coloured plates and engravings are attached to each annual volume of the "Proceedings," to illustrate the new or otherwise remarkable species of animals described in them. Among such illustrations, figures of the new or rare species acquired in a living state for the Society's Gardens are often given.

The "Proceedings" for each year are issued in four parts, on the first of the months of June, August, October, and April, the part published in April completing the volume for the preceding year.

The "Transactions" contain such of the more important communications made to the scientific meetings of the Society as, on account of the nature of the plates required to illustrate them, are better adapted for publication in the quarto form. They are issued at irregular intervals.

Fellows and Corresponding Members, upon payment of a Subscription of £1 1*s.* before the day of the Anniversary Meeting in each year, are entitled to receive all the Society's Publications for the year. They are likewise entitled to purchase the Publications of the Society at 25 per cent. less than the price charged for them to the Public. A further reduction of 25 per cent. is made upon purchases of Publications issued prior to 1871, if they exceed the value of five pounds.

Fellows also have the privilege of subscribing to the Annual Volume of the 'Zoological Record' for a sum of £1 (which includes delivery in the United Kingdom), but this privilege only holds good if the subscription is paid before the First of December in each year.

Such of these publications as are in stock may be obtained at the Society's Office (3 Hanover Square, W.), at Messrs. Longmans', the Society's publishers (Paternoster Row, E.C.), or through any bookseller.

February, 1901.

P. L. SCLATER,
Secretary.

TRANSACTIONS

OF

THE ZOOLOGICAL SOCIETY OF LONDON.

VOL. XVI.—PART 2.

LONDON:

PRINTED FOR THE SOCIETY,

SOLD AT THEIR HOUSE IN HANOVER-SQUARE;

AND BY MESSRS. LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

August 1901.

Price 15*s*.

Taylor and Francis, Printers,] [Red Lion Court, Fleet Street.

cancelled

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

	To Fellows. £ s. d.	To the Public. £ s. d.
VOLUME I. (1833–1835, containing 59 Plates) . . Price	3 13 6	4 18 0*
VOLUME II. (1835–1841, containing 71 Plates) . . „	4 0 0	5 6 6*
VOLUME III. (1842–1849, containing 63 Plates) . . „	3 8 3	4 11 0*
VOLUME IV. (1851–1862, containing 77 Plates) . . „	6 2 0	8 2 6†
VOLUME V. (1862–1866, containing 67 Plates) . . „	5 4 3	6 19 0†
VOLUME VI. (1866–1869, containing 92 Plates) . . „	11 5 0	15 0 0†
VOLUME VII. (1869–1872, containing 73 Plates) . . „	10 4 0	13 12 0†
VOLUME VIII. (1872–1874, containing 82 Plates) . . „	9 8 3	12 11 0†
VOLUME IX. (1875–1877, containing 99 Plates) . . „	12 1 6	16 2 0†
VOLUME X. (1877–1879, containing 95 Plates) . . „	10 0 3	13 7 0†
GENERAL INDEX, Vols I. to X. (1833–1879) . „	0 7 6	0 10 0
VOLUME XI. (1880–1885, containing 97 Plates) . . „	9 12 0	12 16 0
VOLUME XII. (1886–1890, containing 65 Plates) . . „	5 8 0	7 4 0
VOLUME XIII. (1891–1895, containing 62 Plates) . . „	6 8 3	8 11 0

* No copies of these volumes remain in stock.

† Only complete copies of these volumes are left in stock.

Continued on page 3 of Wrapper.

II. *Contribution towards a Knowledge of the Osteology of the Pigmy Whale* (Neobalæna marginata). *By* Frank E. Beddard, *M.A., F.R.S., Prosector and Vice-Secretary of the Society.*

Received May 23, read November 20, 1900.

[Plates VII.–IX.]

The earliest description of any part of this Whale is, so far as I am aware, to be found in Dr. Gray's account of the Cetacea collected during the voyage of the 'Erebus' and 'Terror'[1]. In that memoir he described and figured the baleen of the creature, which was known from three plates, obtained off Western Australia, and now in the collection of the British Museum. These measured 20 inches in length, and were noted as remarkable on account of their "pure white" colour. The baleen, Dr. Gray remarked[2], "is much smaller and broader compared with its width at the base than, and is different in colour from, the baleen of any of the other species [of *Balæna*]." He adds to this that it "is of nearly the same structure as that of the Greenland whale." Dr. Gray's descriptions of new forms of whales, based upon fragmentary portions of their hard parts, were seldom so fortunate as this particular identification of the plates of whalebone with an animal unknown to science. It was by him retained in the genus *Balæna* in the 'Catalogue of Seals and Whales.' Gray was fully justified, and not long afterwards, by further discoveries of this whale.

In 1869 Hector[3] described and figured a skull of a young example of the same whale. Upon this skull Dr. Gray founded a new genus for its reception, to which he gave the name of *Neobalæna*[4].

Later on Sir James Hector appended some "Notes on the Cetacea in the Colonial Museum, Wellington," to a paper by Dr. Knox "On the Balænidæ, or Whales with Baleen"[5]. In the course of these notes upon the subject of the present article measurements and figures of the skull of *Neobalæna* were given, and the author identified the animal with that originally described by Gray in the following concluding

[1] Zoology of the 'Erebus' and 'Terror,' 1846, p. 48, pl. i. fig. 1. See also Cat. Cetacea B. M. 1850, p. 14, and P. Z. S. 1864, p. 200.

[2] Catalogue of Seals and Whales in the British Museum, 1866, p. 90.

[3] Trans. New Zealand Inst. ii. p. 26, pl. ii. B. figs. 1–4. See also Ann. Nat. Hist. v. p. 221, and vi. p. 155, figs. 1 & 2.

[4] Supplement to the Catalogue of Seals and Whales, 1871, p. 39.

[5] Trans. New Zealand Inst. ii. p. 21.

sentence to his essay :—"From the character afforded by the baleen of this specimen I conclude that it is the head of the *Balæna marginata*, Gray, or West Australian Whale."

The skull is figured in three views, and there can of course be no doubt that the identification of Hector was perfectly true.

In a contribution to the same journal as that from which we have just quoted, Dr. Gray [1] gave some further notes upon *Balæna marginata*, establishing it as the type of his new genus *Neobalæna*. The paper is reprinted from one published in the Annals & Magazine of Natural History' [2], and is reproduced in Dr. Gray's full account of *Neobalæna* in the 'Supplementary Catalogue of Seals and Whales in the British Museum.'

Dr. Gray had evidently some justification for pointing out that his separation of the whale by the characters of its whalebone have been fully borne out by the characters of the skull as described by subsequent observers. It is doubtful, however, whether this position is strengthened by his statement that "*Physalus antarcticus*," also differentiated by the characters of its whalebone, has turned out to be a distinct form of Rorqual.

Dr. Gray's definition of the genus, founded upon the skull and the whalebone, was as follows :—

"Skull rather depressed ; brain-cavity nearly as long as the beak, depressed, much expanded at the sides, with a very deep notch on the middle of each side over the condyles of the lower jaw, and with a subtriangular crown-plate. The nose as broad as the expanded brain-cavity at the base, attenuated to a fine point in front and slightly arched downwards. Lower jaw laminar, compressed, high ; the upper edge thin, and inflexed the greater part of its length, erect in front ; the lower edge inflexed in front, the rest of the edge being simple. The baleen elongate, slender, several times as long as broad, with a fringe of a single series of fine fibres ; enamelled surface smooth and polished, thick."

The skull to which this description refers is that described by Sir J. Hector, and was obtained on the island of Kawau near New Zealand. The figures given by Hector are reproduced by Gray in his 'Supplementary Catalogue.' It is an incomplete skull wanting the end of the snout and the lacrymal bone.

A few years later another skull was described by Sir James Hector [3] from the Auckland Museum. It was that of "a young calf," and measured 2 feet 11 inches. The baleen is described as "yellowish white." Hector observes that the whale

[1] "Notes on the Skull of *Balæna marginata* described in the Transactions of the New Zealand Institute, vol. ii. p. 21, as the type of a new Genus *Neobalæna*," Trans. New Zealand Inst. iii. p. 123.

[2] 1870, vol. v. p. 221, and vi. p. 155, figs. 1 & 2.

[3] "Notes on New Zealand Whales," Trans. New Zeal. Inst. vii. 1875, p. 251.

"appears to be found on all parts of the coast, but is described by the whalers as of rare occurrence." It was held by one "qualified informant" to be identical with the rather mysterious "Scrag Whale," a creature which has not been satisfactorily identified with any known form. I hope, however, on a future occasion to have the opportunity of saying something about the latter whale, which may be the Grey Whale of California.

Some little confusion as to possible synonyms of this whale has been introduced by Dr. Gray. In a paper dealing with *British* Cetacea (the italics are necessary) the author adds some details [1] to his earlier notes [2] on the so-called *Balæna* (*Caperea*) *antipodarum*.

These details consist in a description of the tympanic bones of a *Balæna* identified with that species, which were received from Otago, New Zealand. Nothing is there said of the size of these bones. The figures were subsequently copied into the 'Catalogue of Seals and Whales' [3], but again without measurements. These ear-bones, however, were regarded as those of a specimen 60 feet long, to which dimensions it does not appear at all likely that *Neobalæna marginata* ever arrives. Yet in a third reference to this ear-bone, Dr. Gray, though quoting Hector [4] to the effect that it belongs to *Neobalæna*, refers to a skeleton in the Paris Museum as wanting the ear-bones and as being that of a *Eubalæna antipodarum*. The coincidence—not very remarkable—seems hardly worth mentioning, since it was perfectly apparent that there could be no conceivable confusion between the two whales from the investigations of van Beneden and some others who are duly quoted by Gray.

Having thus entered into the matter of the ear-bone, stated by Hector to be that of *Neobalæna*, Dr. Gray unexpectedly observes: "In these remarks I have taken no notice of the Pigmy Right Whale (*Neobalæna marginata*) found in New Zealand and West Australia, because that is at once known from all the others by its small size."

On a later page (P. Z. S. 1873, p. 143), however, the synonymy is correctly [5] given as:

Neobalæna marginata, Gray, Cat. Seals and Whales, p. 90, &c., &c.
Caperea antipodarum, Gray, ibid. p. 101.

In the paper which has just been quoted, Hector refers to a description, contained in a letter written to him by Mr. Traill, of the external characters of this whale, as he correctly assumed and later on proved it to be. It was captured among a large school of

[1] "On the Cetacea which have been observed in the Seas surrounding the British Islands," P. Z. S. 1864, p. 195.

[2] Zoology of the 'Erebus' and 'Terror,' and in Dieffenbach's 'New Zealand,' p. 101.

[3] "Notice of a Skeleton of the New Zealand Right Whale, &c.," P. Z. S. 1873, p. 133.

[4] Ann. & Mag. Nat. Hist. 1873, vol. xi. p. 108.

[5] Correctly, that is to say, as regards *specific* name: for on the page of the Catalogue first quoted it is called "*Balæna marginata*."

Blackfish—a somewhat vague term for a whale, but apparently here meaning a species of *Globicephalus*. The animal was 15 feet 3 inches in length, and of a black colour with a light stripe on the belly. The rest of the description may be given in Sir James Hector's own words:—"Pectoral fins situated immediately behind the head, each being 1 foot 3 inches long. 230 plates of baleen on each side, the largest being 18·5 inches by 1·8 inches at base and 0·1 inch thick; colour of baleen yellowish white with a dark margin. The ribs are at least seventeen pairs, and are very oblique. Most of them are nearly straight, broad, and flat, and very small towards the point of attachment, the form being suggestive of short swords or paper-knives, and from their shape and light curvature very unlike ribs. The sternum is singular, bearing a striking resemblance to a scutcheon, and appearing to have had only one rib-attachment on each lateral border. The seven cervical vertebræ were thoroughly ankylosed."

Mr. Traill held the whale to be a Finback (=*Balænoptera*), apparently because of the dorsal fin, to which Sir James Hector does not allude in his transcription of Mr. Traill's remarks, but refers to afterwards in characterizing the whale. The skeleton of this individual came later into Hector's hands and was briefly described by him with a number of illustrations in a "Postscript" to the same paper. The skeleton did not, however, arrive in a complete condition, as is evidenced by the fact that Hector only describes 15 pairs of ribs, while Traill asserted that there were 17 at least. This skeleton is now in the Natural History Museum in London. A large number of the important points are noted by Sir James Hector. I have, through the kindness of the Director of the Natural History Museum, been able to study this example and also a much finer and apparently adult or nearly adult whale of the same species. This specimen was purchased in January 1886 of Dr. Julius v. Haast. Upon both of these some few notes have been made and published by Sir William H. Flower and Mr. R. Lydekker in their 'Mammals Recent and Extinct.' I have myself dealt briefly with this form in 'A Book of Whales' [1].

The skeleton described by Sir James Hector is so clearly that of a young animal, that it would be impossible, or at least not at all desirable, to draw from its study a final definition of the characters of this remarkable genus. Some of the characters are plainly due to immaturity and would deceive no one; others, on the other hand, would not be known to be those of immaturity, unless an adult skeleton were there for purposes of comparison. Sir James Hector uses, for example, the features of the sternum in his description of the distinguishing characteristics of the genus. It certainly bears no obvious signs of immaturity; but at the same time its entirely different shape from the sternum of the large individual shows that this part of the skeleton does undergo some changes during the process of its complete ossification, unless, indeed, it be the case that the two individuals in the Natural History Museum are really of different species; but this conclusion hardly seems likely in view of the

[1] London, John Murray, 1900.

many close agreements which they present. The shortness of the neural spines of the vertebræ—although clearly partly at least due to youth, as is evidenced by the rough edges which they show, indicating the existence of some unossified cartilage—might not be regarded as entirely uncharacteristic of the species were it not for the second specimen. Length of neural spines is sometimes a character of importance in the Cetacea. In the larger specimen the great length of the neural spines is a very distinguishing feature of the skeleton, and is no doubt a character of the genus or species. The slightly different form of the scapula in the two whales is another point to which attention might be directed as evidence of specific difference; but it hardly, to my mind, amounts to a sufficiently marked variation, and might also be—probably is—due to different stages of ossification.

I now proceed to a description of the skeleton of *Neobalæna*, which is mainly drawn from the larger individual at South Kensington.

The Vertebral Column.

The total number of vertebræ possessed by the larger of the two specimens is 43, which are thus distributed among the several regions :—

C. 7. D. 18. L. 2. Ca. 16=43.

The cervical vertebræ (Pl. IX. fig. 3), as in *Balæna*, form a fused mass, and the fusion is very thorough though not absolutely complete. The spinous processes of all seven are completely fused. A single broad plate of bone, rounded anteriorly and concave posteriorly, represents the seven spinous processes of the cervical vertebræ. Laterally, however, the fusion is not so thorough. The first five are quite consolidated; but behind this mass the backwardly projecting process which corresponds to the metapophysis of the dorsal vertebræ is quite obvious for the two remaining vertebræ of the series. The upper bars of the transverse processes of these vertebræ are longest in the atlas; from this vertebra they gradually decrease in size up to the fourth. The process in question of this vertebra is pretty nearly of the same length as are those of the following ones. The lower transverse processes of the vertebræ are fused into a thick plate which is concave on its upper face, that turned towards the upper transverse processes. It is one solid piece, and no traces exist of its formation out of various component parts. The anterior end of the plate of bone projects more than the middle and hinder portions; there is thus a correspondence with the upper transverse processes. The total length of the seven cervical vertebræ is about equal (a little less than) the length of the succeeding three dorsals.

The dorsal vertebræ, as already mentioned, are eighteen in number. The first of the series (the lower vertebra in Pl. VIII. fig. 2) is much less than those which follow; its transverse processes only reach out to very nearly the same level as those of the immediately preceding cervicals. The transverse processes of this and of the three following dorsals are thickish from above downwards and not wide; the thickness

of these processes diminishes in the succeeding vertebræ, and culminates with number nine of the series, which is thin and lath-like; in all the following dorsals the thin and wide character of the transverse processes exists; these processes go on without much change, through the lumbars and caudals, becoming, however, much shorter as the end of the series is approached. The last traces of transverse processes are evident on the fourth caudal, after which there are no recognizable projections.

The spines of the dorsal vertebræ rise up to the sixth (Pl. VII. *D.* 6); this vertebra is the first to show a backward inclination of the spine; the slope of the processes increases up to the sixteenth, after which they continue to slope at much the same angle. The length of the spines begins to diminish after the fourteenth dorsal. On this vertebra the length of the spinous process is 12 inches. They are recognizable until the beginning of the caudal series (Pl. VIII. fig. 3). On the second caudal vertebra the anapophyses are on a level with the spinous process, which is still perfectly separate from them. On the sixth caudal vertebra the spine and the anapophyses form a low oval elevation of which the component parts are no longer distinguishable. The neural canal also is persistent up to this point as a canal. On the seventh caudal this canal has become a groove upon the dorsal surface of the vertebra. There is no groove or canal from this point till the end of the body. The metapophyses bearing the quite rudimentary posterior zygapophyses are but little pronounced. They appear to end with the fourth dorsal vertebra. They do not embrace the anterior zygapophyses but are set above them. The anapophyses bearing the anterior zygapophyses begin faintly with the first dorsal. They are recognizable, as already said, up to the sixth caudal, but they do not grasp the spinous process of the vertebra in front after the first lumbar. The articulation, however, between these processes and the preceding vertebra is always very faint. Reckoning the first vertebra which bears chevron-bones as the first caudal, the skeleton will have only two lumbar vertebræ, the smallest number known in any whale. There are 6 chevrons (Pl. VII.), of which the last only is divided into two pieces, not ankylosed together.

The transverse processes of the dorsal vertebræ arise at first from the sides of the neural arch; later they spring from the centrum of each vertebra. The sixth dorsal vertebra is the first of the series of those whose transverse process is most unmistakably a process of the centrum. The vertebra in front of this is nearly, but not quite, in the same condition; there is still a trace of the origin from the neural arch discernible. In front of this vertebra the transverse processes are quite distinctly processes of the neural arch.

The vertebral column of this whale shows a certain number of intermediate characters. The shortness of the vertebral column, *i. e.* the comparative fewness of its component vertebræ, is apparently a peculiarity of this genus. But it throws no particular light upon its affinities. It is apparently to some extent a question of size; at least this may be the case, for in the small *Balænoptera rostrata* there are as few as

50, 48, or even possibly 46. The large species, *B. musculus*, on the other hand, has as many as 62 vertebræ in its skeleton. In the Right Whales the figures given by van Beneden and Gervais are 53–58. Thus *Neobalæna* has the shortest vertebral column of the three genera considered. The shortness, it will be observed, is chiefly in the lumbar region, which, consisting as it does of at most 2 vertebræ, is the shortest lumbar region, not merely of any Whalebone Whale, but of any whale at all. *Inia*, with 3 of these vertebræ, only just betters it. The 18 dorsals, again, are in excess of any other of the allied whales.

The cervical mass is completely fused, as in the Right Whales. So far *Neobalæna* is distinctly referable to this division, and differs from the Rorquals. The fusion of the vertebræ appears to go on during life, becoming more complete, as is shown by the two skeletons dealt with here; the details need not be recapitulated. The fusion seems to be more thorough than in *Balæna*. At any rate, the skeleton of an adult *Balæna* figured by van Beneden and Gervais, which shows no epiphyses in the vertebral column, exhibits distinctly the lines of separation of all the cervicals from top to bottom of the neural arch. The same may be said of the cervical mass of an adult Greenland Whale figured by the same authors. In this skeleton, however, the epiphyses of the vertebræ have not entirely become coalesced. Another distinguishing character of this whale appears to be the great wing-like masses formed by the lower transverse processes. In short, it will be apparent from the illustrations that in this region of the vertebral column *Neobalæna* carries to an excess the characteristics of *Balæna*.

It must be noted, however, that though on the whole the cervical mass of *Neobalæna* most resembles that of the Right Whales, there is one feature in which it disagrees with the characteristics of those vertebræ in the genus *Balæna* and comes rather nearer to the Rorquals. In *Balæna* the lower transverse processes of the cervical mass are often reduced, and the second and following ones are much feebler than the first or the first two. In the Rorquals, on the other hand, the equally strong development of the lower transverse processes of these vertebræ is a distinctive mark. They are well developed and equally so in all of them; but the processes, like the vertebræ themselves, preserve their independence. It is perhaps permissible to call attention to this as a point of affinity between *Neobalæna* and *Balænoptera*, though on the whole the differences between the cervical region in *Neobalæna* and in other Rorquals are more striking than the likenesses.

The most remarkable feature about the dorsal series of vertebræ is of course the fact that the first dorsal appears to have no rib. Its transverse process does not stand out as far as those of the succeeding vertebræ; there is thus hardly room for a rib except a very minute one, which might conceivably have got lost. It is to be remembered, however, that in both skeletons this rib is wanting, and indeed the next one also in the immature skeleton. Furthermore, the first actual rib (the second of a hypothetical series) articulates with the sternum, as is always the case with the first vertebra

in these animals. Nor is there apparently any room on that bone for the articulation of a rib lying in front of this. This is a condition quite curiously the reverse of that which often obtains in Rorquals (and other Cetacea), where the first rib is two-headed and, indeed, partly double through its extent, being apparently formed by the union of the ordinary first rib and a cervical rib. In *Neobalæna* the ribs are decreasing in number, and in consequence the first dorsal is small. It is, however, in the fully-grown animal incomplete above, as it is in the immature skeleton, where the neural arches do not meet. This latter fact is duly noted by Hector.

It has been mentioned that the first six dorsal vertebræ only, and the last of these hardly, have the transverse processes arising from the neural arch itself. In *Balæna* the series of vertebræ in which the transverse processes arise thus is a longer one. The first ten dorsals in *Balæna australis* are provided with transverse processes which definitely arise from the neural arch; after that point they more and more distinctly arise from the centrum of the vertebra. The arrangement in *Neobalæna* is more like that of *Balænoptera*. In *Balænoptera laticeps* (?=*B. sibbaldi*) the sixth dorsal vertebra has a transverse process arising from the centrum. The same appears to be the case with *Balænoptera rostrata*.

The Scapula.

The scapula (Pl. VII., *Sc.*) presents considerable differences of form in the two specimens. In the younger specimen it is much as was figured by Sir James Hector. The bone is very elongated and not at all high. The highest point, moreover, is not the middle of the superior border of the blade. The shape, in fact, is far from regularly fan-like. A series of measurements showed that the anterior end of the upper border is the highest part of the scapula. It is slightly depressed in the middle. So very much does the posterior border slope directly backwards from the glenoid cavity, that it seems to be almost in a straight line with it and with the acromion. Though I have seen no scapula in any allied form in which this is the case, it appears that even in *Balæna*, which has a particularly high scapula, the acromion is actually in the same straight line, or very nearly so, with the posterior border of the shoulder-blade. Hector has observed this, but has not emphasized the fact that the acromion and the posterior border of the scapula are in the same straight line and that there is so far no divergence from the characters of that bone in other Whalebone Whales. As to the elongation of the shoulder-blade, I found that the measurements of length and extreme height (not, as already mentioned, in the middle of the bone, but near to the anterior end, and, moreover, an oblique line ending at the middle of the glenoid cavity) are for the right-hand bone $12\frac{1}{2}$ inches as against 7 inches in height. The left-hand scapula was a little, a very little, different. The corresponding measurements were 13 and 7. Taken in the middle of the superior border and drawn at right angles to that border down to the margin of the glenoid cavity, the diameter of the scapula was not more

than $6\frac{1}{2}$ inches. The corresponding measurements of some individuals of *Balænoptera* were as follows :—

Balænoptera rostrata, 15×9.
Balænoptera "huttoni," $14\frac{1}{2} \times 8\frac{1}{2}$ [1].
Balænoptera musculus, $50\frac{1}{2} \times 33$.

It is clear therefore, from a comparison between these measurements, that the scapula of *Neobalæna marginata* is distinctly longer in proportion than it is in *Balænoptera*; *à fortiori* it is much longer in proportion than is the scapula of *Balæna*, which, as is well known, is a high scapula.

The blade-bone is thin and slightly curved, when viewed from above, in an S-like direction. It is neither definitely concave nor convex on either side. The comparatively wide flat acromion is about three times the width of the coracoid process. When the scapula is looked at from above, the coracoid is seen to project very strongly inwards, and the acromion, though but slightly, outwards. The effect of the foreshortening is that the scapula seems to end anteriorly in three prongs. In the Rorquals the same state of affairs is to be noticed; and, as in *Balæna australis* the coracoid projects distinctly outwards, we have here another feature in which *Neobalæna* is more akin to the genus *Balænoptera* than it is to *Balæna*.

In the larger and more mature specimen the scapula was a little different in form. It has the more regularly fan-shaped outline of that bone in the Rorquals; but it has not the appearance of so great an antero-posterior elongation as in the smaller *Neobalæna*. Measurements confirm this appearance.

The two blade-bones of this individual only differ in the fraction of an inch, 20 and $\frac{6}{8}$ inches was the length as against 11 and $\frac{6}{8}$ inches vertical diameter, and $13\frac{1}{4}$ oblique. Thus the proportions in this individual are not so un-Rorqual-like. But at the same time it will be noted that while in *Balænoptera* the height is to the length as $1 : 1\frac{2}{3}$, the same proportions in the larger *Neobalæna* are as $1 : 1\frac{3}{4}$; thus showing that there is really the same difference here as in the smaller example, though not quite so pronounced. It may well be that the indented upper margin of the scapula of the smaller specimen indicates incompleted ossification; it appeared rough to the touch, which is so far evidence, as bone embedded in cartilage, which will continue to ossify, ends abruptly in that way.

The Pectoral Limb.

As will be seen from an inspection of Plate VII., the fore-limb of *Neobalæna* is of relatively small size. Its proportionate length compared with the length of the body of the creature is small as compared with that of the Rorquals, and smaller still when

[1] I enclose the specific name in inverted commas since the name on the label attached to the specimen is not certainly correct. I believe it to be *B. rostrata*.

compared with that of the Right Whales. It need hardly be pointed out how very different is this limb from the great paddles of *Megaptera*. It is, however, apparently four-fingered as in the Rorquals; no trace of the additional fifth finger of the Right Whales was to be observed.

The humerus is short as compared with the radius. The measurements of the smaller individual were 4 inches for the humerus, and 6 for the radius. The proportions are a little different in the larger specimen.

I append for the purpose of comparison a few corresponding measurements from other Whalebone Whales:—

	Humerus. in.	Radius. in.
Balænoptera rostrata	$7\frac{1}{4}$	$10\frac{1}{2}$
B. "huttoni" [1]	7	$10\frac{1}{2}$
B. sibbaldi	15	28
B. musculus	12	22
B. musculus	18	31
Balæna australis	15	$15\frac{1}{2}$
Megaptera	13	34

It seems to be plain, therefore, that the arm of *Neobalæna* is like *Balænoptera* in its proportions, just as the hand resembles that genus in being four-fingered. As the ends of the digits are evidently missing, it seems to be useless to enter into any description of the component bones of the hand.

Ribs.

The adult or nearly adult skeleton of this whale possesses 17 pairs of ribs, the largest known number in any Whalebone Whale: the nearest approach is seen in *Balænoptera sibbaldi*, where there are 16; indeed this latter may possess 17, since the first rib is occasionally double, a cervical being fused with it. As already mentioned, the ribs begin with the second dorsal vertebra, the first having apparently no rib. It is remarkable that in the Cetacea we find precisely what is found in the Manatee and the Sloth—the decrease of the cervical region by the presence of an additional rib belonging to the last cervical, and the increase of the cervical region by the apparent dropping of a rib.

As is always the case in the Whalebone Whales, only one rib articulates with the sternum. This rib (Pl. IX. fig. 6) is very broad below, where it expands into its articular face; but the broadening is gradual, not sudden; and it is only the proximal end of the rib which equals the succeeding ribs in diameter. This broadening is very marked indeed, and is more marked than in any other Whalebone Whales. The Right Whales come nearer in this particular to *Neobalæna* than do the Rorquals. The general form of the ribs undergoes some modification in the series. The first rib is simply

[1] See footnote to p. 95.

curved; the next four (Pl. IX. figs. 4, 5) are sharply bent at right angles at a point some distance from the capitulum. The bending in the last of these is not so marked. It more approaches the regular curve of the succeeding ribs. In the ribs further towards the end of the series (Pl. IX. fig. 7) the curvature is less and less marked, and the rudimentary last rib is almost quite flat. At the angle where the rib bends down it is flat and compressed, as if the bone had been squeezed between the thumb and first finger. This sharpish edge is recognizable on ribs three to five inclusive, and even to a trifling extent in number six. The anterior set of ribs are moderately flattened in a plane at right angles to the long axis of the body.

The last of the series are much more flattened, but in a plane parallel to that axis. The intermediate ribs have a twist about one fourth of the way down; the distal portion of the rib gets to be expanded in a plane parallel with the long axis of the body, while the head end retains its parallelism to axes at right angles to the long axis of the body. This twist is gradually rectified as we progress from the anterior to the posterior ribs.

The peculiar form of the first rib has been mentioned. The six following ribs are narrow in diameter. The eighth has a greatest diameter of $3\frac{1}{4}$ inches; the greatest breadth is attained by the tenth, which is some $5\frac{1}{2}$ inches in diameter. This is maintained through the next four, after which the breadth diminishes and the small last rib is very narrow, and indeed altogether rudimentary. The very different appearance of ribs from different regions is illustrated in the accompanying drawings (Pl. IX. figs. 4–7). None of the ribs reach the bodies of their vertebræ, a feature in which of course *Neobalæna* agrees with other Mystacoceti. But several of them have a distinct capitulum and tuberculum with an intervening neck. In the first rib these could barely be distinguished. Ribs 2–6 have both capitulum and tuberculum quite plain; these are most obvious, because separated by a longer neck, in vertebræ 3 and 4 (Pl. IX. figs. 4, 5); in them the neck measured about 5 inches in length.

Another feature which the ribs of this whale share with those of other Whalebone Whales should be noticed. In the posterior and more rudimentary bones of the series the rib gradually decreases in diameter, not only at the distal free end, but also at that end which is nearest to the vertebral column. It does not appear, indeed, that during life the thin commencement of many of the posterior ribs ever came into direct relations with the vertebral column. It is, in fact, the middle part of the rib which is alone ossified, the two ends having apparently been represented by fibrous or cartilaginous tissue.

The great breadth and the large number of the ribs of *Neobalæna* give a suggestion of a Sirenian to this, as I believe, primitive form of Whalebone Whale. The likeness is here only pointed out; it is not possible to build any views as to the affinities of the Cetacea upon it.

In the introductory anatomical sketch of their great work on the Osteology of

Whales, MM. van Beneden and Gervais make a statement which the structure of the present species of whale, as will be seen by a glance at Plate VII., does not bear out, and perhaps in a more marked degree than some other Whalebone Whales. The authors remark that in Whales in general, not only in Whalebone Whales—"Les premières (côtés) sont toujours les plus larges et les plus courtes." This is most clearly untrue of *Neobalæna marginata*, and is really not absolutely true of all other whales, though unquestionably it is of the great majority.

In a quite unexpected way *Neobalæna* resembles not so much other Balænidæ as it does many Toothed Whales as regards one character of its ribs. In the former group the ribs are, as has been pointed out by van Beneden and Gervais, less flattened and distinctly more rounded than they are in the Odontocetes. This flattening is carried to an enormous degree in *Neobalæna*, which thus departs very widely from its nearest allies among whales. That there happens to be in this particular a resemblance to that group of whales with which *Neobalæna* has plainly no obvious affinities, cannot but be regarded as a caprice of structure of no account in considering the affinities of our whale.

As to other likenesses and differences from other Whalebone Whales which *Neobalæna* shows in the form of its ribs, the following comparisons seem to be of perhaps some importance, in addition, of course, to the highly remarkable fact, already emphasized in connection with the vertebral column, of the commencement of the series of ribs with the *second* dorsal vertebra.

In *Balæna australis* the first rib is much curved round at its articulation with the vertebral column, very much more so than in *Neobalæna*, but it must be said to lack a "neck," since it is the extremity of the bone which is attached to the vertebra—"Le col et la tête manquent également du reste aux premières côtés," is the statement of the authors of the 'Ostéographie des Cétacés.' The last five ribs of that whale are incomplete and possess no neck. There are thus nine which have a clearly developed capitulum, though of course they do not reach the bodies of the respective vertebræ. In the other species of *Balæna*, *B. mysticetus*, there are but thirteen pairs of ribs. Of these the first two pairs have no trace of head or neck. The last two are similar in so far as this point is concerned. There are therefore here at any rate nine ribs with a neck. The number is not very different from that of *Balæna australis*. In *Neobalæna* it is plain that a considerable number of ribs have acquired the secondary character of possessing both tuberculum and capitulum.

Turning to the Rorquals we find quite a different state of affairs. In *Megaptera*, where there are fourteen pairs of ribs, only the third and the fourth agree to differ from the rest by the possession of a distinct neck. But there are traces of the division in at any rate the two following ones. In *Balænoptera musculus* Sir W. H. Flower described [1] the ribs in the following words—"The first rib is simple . . . The second

[1] P. Z. S. 1864, p. 415.

and third have capitular processes which reach nearly to the bodies of the vertebræ, that of the second is rather the longest . . . . The neck becomes rudimentary in the fourth and obsolete in the fifth and all succeeding ribs." In "*Physalus latirostris*" (which appears to be identical with what is now known as *Balænoptera sibbaldi*) there are fifteen pairs of ribs. But though there is one pair more than in the last species the ribs are less modified. The second and third, according to Flower, have well-developed capitular processes; but these processes become "nearly obsolete" on the fourth.

The small *Balænoptera rostrata* has, in correspondence with its diminished size, fewer ribs than its gigantic allies. It has only eleven pairs of these bones. MM. van Beneden and Gervais find from an examination of skeletons that, as in other Rorquals, the first pair are without a capitulum. It is not necessary to go into further details concerning the characters of the ribs in the Whalebone Whales. I may say that the facts given above have been verified by me in the skeletons of these whales in London. The principal generalization to be drawn from these facts is that the genus *Balænoptera* has a more imperfect series of ribs than the genus *Balæna*. Fewer ribs in the former have the two heads of the typical mammalian rib. Now in this feature it is clear that *Neobalæna* comes nearer to *Balænoptera* than to *Balæna*. It is, in fact, somewhat intermediate between the two. We might presume that *Neobalæna* offers a more primitive state of affairs than either of the remaining families of Right Whales from certain points of view. It is perfectly clear that the original condition of ribs is shown (so far as concerns the Mammalia) in the Monotremata. In that group the ribs retain their primitive intercentral position, arising only from the bodies of the vertebræ, and having no connection with the transverse processes of the vertebræ. It does not, however, follow from this that *Balænoptera* and *Megaptera* exhibit the least archaic conditions, because there are so few ribs which retain at any rate traces of the presumably primitive connection of the ribs with the centra of their vertebræ. It seems to me that Prof. Max Weber [1] has shown conclusively, in opposition to Prof. Albrecht [2], that we must look upon whales as definitely "eutherian" mammalia and as not representing in any way the problematical "promammalia." If that be so, the ribs of whales are derived from those of some terrestrial mammal in which both central and tubercular heads were present. The loss of the former and the feeble development of the latter are to be explained by respiratory exigencies, necessitating an imperfect articulation with the vertebræ at both points.

This allows of course of a greater expansion of the chest-cavity and a consequent completer filling of the lungs with air. If it could be shown that *Neobalæna* is a

[1] Weber, "Ueber die Cetoide Natur der Promammalia," Anat. Anz. ii.

[2] Albrecht, "Ueber die Cetoide Natur der Promammalia," ibid. i. p. 338.

whale which dives more persistently and for greater periods of time than any of its allies, the large number of ribs and the fact that so many of them are so imperfectly attached to the vertebral column would be intelligible. But we have no knowledge of the habits of this whale which could allow of any such a theory.

The Sternum.

The great care which must be exercised in using the sternum as a character of generic or specific importance in whales, is illustrated by that of the present species. Sir James Hector correctly figures the sternum of the individual studied by himself, and well describes it as "bearing a striking resemblance to a scutcheon." It has in fact precisely this form in the smaller and immature skeleton of *Neobalæna* in the British Museum. The anterior border projects in the middle line, and again on both sides, while the margins are rounded and converge slightly posteriorly. On the other hand, as will be seen from the drawing which I exhibit here (Pl. IX. fig. 2), the sternum of the larger and more mature skeleton is quite different. It has, as will be seen, somewhat the form of a Maltese cross. The anterior border, the posterior border, and both sides are excavated at points exactly, or very nearly exactly, opposite to each other, so that on the whole a cross-like form is produced. The anterior excavation is the deepest of the four. The two lateral excavations are rather more pronounced than that of the posterior border. In the figure to which I have just referred, the sternum is viewed a little in profile owing to the position of the skeleton and the impossibility of getting a direct dorsal view. But no confusion can arise in consequence as to the shape of the bone and the proportions of its different parts. Now it is curious that the sternum which appears to be the more unfinished, *i. e.* the least ossified, is that of the demonstrably older individual. The filling in of the anterior excavation with bone and its projection forward would certainly appear at first sight to be a mark of age. It may still be the case that the specimens are really of different species. But other considerations forbid this assumption in my opinion. The variability of the form of the sternum is only another illustration of the fact that degenerating organs tend to vary considerably. But the variations of form of this organ seem to be greater in *Neobalæna* than in any other Whalebone Whale.

The Skull.

As will be seen from an inspection of the large drawing (Pl. VII.), which is illustrative of the entire skeleton of *Neobalæna*, the skull is not large in proportion to the rest of the skeleton. That drawing, it should be explained, is not exactly parallel to the horizon. The position of the skeleton in the Whale Gallery at the Museum rendered it impossible to obtain an accurate horizontal sketch. The amount of obliquity, however,

does not seriously interfere with the understanding of the proportions of the different regions, while it does not at all mask the form of the various parts of the skeleton. The proportions of the length of the skull to that of the entire skeleton including the skull are as 1 : $5\frac{1}{2}$. It will be noticed therefore that the proportions are not those of either of the whales of the genus *Balæna*. The proportions, in fact, are roughly those of any species of the genus *Balænoptera*. The proportion of the head to the trunk has formed in the diagnosis of many naturalists an important feature in the distinguishing of the families Balænidæ and Balænopteridæ, or of the genera *Balæna* and *Balænoptera*, according to the views taken of the systematic arrangement of the Mystacoceti. So far *Neobalæna* is in no sense intermediate; it distinctly resembles the Rorquals.

But the general aspect of the skull is on the whole suggestive of that of *Balæna*. This likeness is of course emphasized by the long whalebone, which extends in the dried skull to a point considerably below the lower margin of the mandible, when that bone is approximated to the upper jaw. The skull as a whole is arched and the rostral part is narrow; this latter feature is well exhibited in the figure (Pl. VIII. fig. 1) which illustrates the skull viewed from above. If this aspect of the skull of *Neobalæna* be compared with the corresponding aspect of the skulls of *Balæna* and *Balænoptera*, the closer resemblance of *Neobalæna* to the former genus will be apparent. For in the Rorquals the rostrum is much broader than in *Balæna*. The length of the rostrum also as compared with that of the rest of the skull is a feature in which *Neobalæna* suggests a true *Balæna* rather than a Rorqual. The rostral portion just about equals in length the back part of the skull. It is not, however, to all appearance quite so long proportionally as it is in the Right Whales; but the difference is in reality due to the narrowness of the frontal bones in *Balæna*, a feature which seems to be if anything less marked in *Balæna australis* than in its Greenland congener, *B. mysticetus*. It is interesting to note that *Neobalæna* is nearer to what we must probably look upon as the less specialized type of Right Whale; less specialized because of its wider range, variability, less arched skull, &c. It is also permissible to point out that the proportions of these different regions of the skull and the degree to which the bones form an arch anteriorly, are more like those of a fœtus of *Balæna mysticetus* figured by MM. van Beneden and Gervais [1] than the adult of either of the two Right Whales. It may be further observed that in the young of *B. mysticetus* the head is not so enormously large in proportion to the trunk as it is in the adult of that whale.

Coming to the details of the skull-structure in *Neobalæna*, we find on the whole a greater likeness to *Balæna*, but that in certain features the characters of the Rorqual appear.

[1] Ostéographie des Cétacés, pl. i. figs. 7, 8.

The vertex of the skull is situated just behind the nasal bones.

The *nasal bones* are not unlike those of other Mystacoceti in their general form. It will be observed from the drawing (Pl. VIII. fig. 1) that they are distinctly asymmetrical when seen from above; the right bones are larger than the left. This drawing, it should be explained, is a copy of the skull of the younger individual.

The *maxillæ* (Pl. VIII. fig. 1, Pl. IX. fig. 1, *Mx.*) are, as usual in these whales, bones of a bent form; the posterior half meets the anterior half at an obtuse angle. The former is much shorter than the latter, the proportions being as 1 : 2. The actual lengths, as measured, are respectively 16 and 33 inches. The form of this bone as regards the proportions of its two halves is like those of the Right Whales and contrasts with those of the Rorquals. In the latter the descending bar of the maxilla, though it reaches below the orbit in *Balænoptera*, as it does in *Neobalæna*, is distinctly shorter, the anterior portion being thus relatively much longer in that genus of whales. Another character of this bone shows in *Neobalæna* a close likeness to what obtains in the genus *Balæna*. There is posteriorly a ridge near to the posterior boundary which curves round, but is of comparatively slight extent, both in *Neobalæna* and *Balæna*. In *Balænoptera*, on the contrary, we find that this ridge is very much more marked, and that it extends further, curving backwards in the direction of the occipital region of the skull, and, as it were, sheltering the frontal bone behind. The maxillæ do not reach the end of the jaw.

The inner angle of each maxilla is prevented by the premaxillæ from coming into contact with the nasals; it extends back, as already mentioned, for a little way beyond the outer portion of the bone, that portion which extends backward being of about the same diameter as the adjacent premaxillary. In *Balæna* there is the same failure of the maxillæ to articulate with the nasals; but the forwardly running portion of the bone is hardly differentiated. The Rorquals, on the other hand, show an entirely different arrangement of these parts. The internal angle of the maxilla is prolonged into a long and narrow process, which extends for a long way backwards and articulates directly with the nasals. There is completed in some of these whales a condition which is only just commencing in the genus *Neobalæna*.

The *frontal* (Pl. VIII. fig. 1, Pl. IX. fig. 1, *Fr.*) bone of *Neobalæna* is, on the other hand, decidedly more like that of *Balænoptera* than of *Balæna*. If the skulls of the two latter genera be compared with each other, it will be noted that they differ markedly in the width of the frontal bones. In the Rorquals these bones are very broad, and thus get an appearance of being much shorter than those of *Balæna*, which are narrow, and, indeed, hardly exceed in width the descending part of the maxilla. Furthermore, their backward inclination in the Right Whale is much more marked than in the Rorqual. As will be seen from the drawings exhibited (Pls. VIII. & IX. fig. 1), the conditions which are to be met with in this region of the skull of *Neobalæna* are quite like those of the Rorqual. The descending part of the frontal, where it

forms the margin of the orbital cavity, is very broad and short relatively to its length. It is, in fact, constructed precisely on the same plan as that of the frontal in the genus *Balænoptera*.

Viewed from above the orbital portion of the frontal bones is decidedly squarish in outline. The length of the anterior side, that to which the maxilla is attached, is pretty nearly the same length as the side which overhangs the actual orbit. The frontal extends so far back that when the skull is looked at from above there is no gap to be seen between the frontal and the squamosal. In the skulls of both *Balæna* and *Balænoptera* this is not the case ; and they are always, and properly, figured as showing a large vacant space between the edges of the two bones mentioned. Otherwise the general outline and indeed the proportions generally and the mutual angles of the borders of the frontals of *Neobalæna* are almost a replica of those of the Rorqual, and correspondingly distinct from those of *Balæna*. It will be observed from an inspection of the drawing exhibited (Pl. VIII. fig. 1) that a forward process of the frontal indents the maxilla, that bone having a corresponding concavity upon its anterior edge which receives the convexity of the frontal. To the inside of this the maxilla extends forwards for a short distance until it is stopped by the median part of the frontal bone, with which it articulates. The convexity thus formed upon the frontal is not, however, very deep. When we compare these conditions with the corresponding ones in *Balæna* and *Balænoptera*, we find that *Neobalæna* is somewhat intermediate, with a stronger resemblance to *Balæna*. In the Rorquals the maxilla extends for a long way forward, while in *Balæna* the edge is nearly straight. Thus *Neobalæna* occupies a midway position with respect to its two allies; but it is decidedly nearer to *Balæna* than to *Balænoptera*.

Lodged between the frontal behind the maxilla in front is the small *lacrymal bone* (Pl. IX. fig. 1, *L.*), which is thin and plate-like. It presents no features of special interest when compared with the corresponding bone in *Balæna* and *Balænoptera*.

The *premaxillæ* (Pl. VIII. fig. 1, *P.Mx.*) of *Neobalæna* reach right to the end of the jaw, from a participation in which the maxillæ are excluded. This is shown both in the lateral and the dorsal view of the skull. They are thin and narrow bones which preserve approximately the same diameter throughout their whole course, being only slightly wider posteriorly than anteriorly. Posteriorly they are widely separated, and leave a wide vacuity in the middle line of the skull above; for the last one-third of their total length they are in contact. They articulate behind with the frontals and with the nasals, and, of course, along the whole length with the maxillæ. The articulation with the nasals is for nearly the entire length of those bones, and, as already mentioned, the premaxillæ and the frontals are the only bones which have a junction with the nasals. Where they embrace the nasals they are bowed inwards. The premaxillæ of *Balæna* offer a few points of difference from those of *Neobalæna*, but on the whole agree with them more closely than do those of *Balænoptera*.

In the first place, the premaxillæ of *Balæna* embrace the whole length of the nasal bones, and even extend beyond them ; in the second place, they appear to be in contact anteriorly for rather a greater extent than is the case with *Neobalæna*. These bones are altogether more prominent upon a dorsal view of the skull than in *Neobalæna*. In the Rorquals the premaxillæ are still more different from those of *Neobalæna*. They only reach the anterior half of the nasal bones, the maxillæ, as already stated, articulating with the latter bones. This is not, however, always the case, for van Beneden and Gervais figure a dorsal view of the skull of *Balænoptera sibbaldi* in which the premaxillæ not only reach the entire length of the nasals, thus cutting them off from the premaxillæ, but extend considerably beyond them. On the other hand, in a skull of *B. rostrata* the premaxillæ stop short of the nasals. These differences, possibly due to the state of ossification of the skulls in question, may therefore be regarded as of less importance than the fact of the great backward extension of the maxillæ, which occurs in all skulls of *Balænoptera*.

The *occipital* bone of *Neobalæna* is remarkable for its great length, which gives to the back part of the skull a much greater extent proportionately than in other Whalebone Whales. This is clearly seen in the drawing which shows the skull when viewed from the side (Pl. IX. fig. 1) more clearly than in that (Pl. VIII. fig. 1) which exhibits the skull from above. The exoccipital regions on either side of the condyles project much further back along the squamosals than in any *Balæna* or *Balænoptera*. Superiorly the occipital is naturally wider behind than in front ; it is ridged along the middle line and terminates anteriorly in a square face of articulation with the frontals. The diameter gradually diminishes from the back part of the skull to the anterior end of the bone. The length of the bone is greater than the width of any part which appears on the dorsal surface of the skull, as is seen in the figure referred to (Pl. VIII. fig. 1).

The posterior contour of the occipital is different from that of either *Balæna* or *Balænoptera*. The lateral parts of the bone jut out considerably beyond the level of the condyles, while in *Balæna* the posterior transverse line of the skull is nearly straight, less so, however, in older than in younger specimens. In *Balænoptera* we find the same relative straightness of the posterior face of the skull. The differences appeared to me, from a comparison of actual skulls, to be rather greater than is depicted in the figures illustrating the ' Ostéographie des Cétacés.' Viewed from above the form of the occipital is not uncharacteristic. For in *Balæna* this part of the bone is as broad as it is long, or nearly so, and of a more rounded form than in *Neobalæna*. In *Balænoptera* the bone is also comparatively short and wide, and, moreover, it does not nearly reach to the anterior end of the orbital plates of the frontal. In *Neobalæna* it very nearly does so, and in this feature the skull of *Neobalæna* is much more distinctly to be compared with that of *Balæna*. Indeed

the great length of the roofing portion of the occipital bones is a very distinctive feature of the whale *Neobalæna* as compared with its immediate allies.

The *squamosal* (Pl. VIII. fig. 1, Pl. IX. fig. 1, *Sq.*) is rather characteristic in its form in this whale. The lower border of the bone projects down behind the glenoid cavity considerably further than it does in front. In this region, indeed, it hardly overshadows the condyle of the lower jaw, there being from before backwards a gradual descent in the margin of the bone. There is, moreover, a much shorter part of the lower margin of the squamosal lying in front of the condyle of the lower jaw than there is behind it. On the whole the genus *Balæna* is most like *Neobalæna* in this particular; in *Megaptera* and in the Rorquals the bone is much wider across the glenoid border, and the half of the border which lies in front of the glenoid cavity is proportionately much longer. This great forwardly directed process of the squamosal is but feebly developed in *Neobalæna*.

Viewed from above, the disposition of the squamosal differs in the three types of Whalebone Whales almost equally, and *Neobalæna* is not any more like *Balæna* than it is like *Balænoptera*. As already mentioned, the occipital projects back for some way behind a line passing through the two occipital condyles, and the backward projection of the squamosal is almost exactly coextensive with the hinder parts of the exoccipitals. This is to a certain degree paralleled in *Balænoptera*, where the two bones end posteriorly at about the same level; but in that genus the projection of the two beyond a line drawn at right angles through the occipital condyles is very much less than in *Neobalæna*. On the other hand, in *Balæna* the squamosal projects back with an extension which is quite as fully marked as in *Neobalæna*, but the exoccipitals do not accompany this backward projection of the squamosal. This statement is at variance with the numerous figures of the skull of *Balæna* seen from above, such as those of Gray in the 'Catalogue of Seals and Whales,' or the figures of MM. van Beneden and Gervais; but all those figures represent the skull viewed in such a fashion that the occipital condyles are entirely or nearly entirely exposed. My own comparison represents the skulls of these three whales viewed more directly from above without a complete exposure of the condyles.

In the arrangement of the *pterygoids* and the *palatines*, *Neobalæna* is much like the Right Whale; in *Balænoptera* the pterygoids have a marked backwardly directed spur; of this there are only traces in *Neobalæna*.

The *lower jaw* of *Neobalæna* is remarkable on account of its great depth. Its curvature is sigmoid, and the symphysis is preceded by a decided dip downwards in the direction of each mandible. The coronoid process is quite feebly marked, but is still perfectly recognizable (as is to be seen in Pl. IX. fig. 1, *C.*). When viewed from above (Pl. VIII. fig. 1) the spoon-shaped outline of the interspace between the two rami of the mandible is seen to be but feebly represented.

The space has comparatively straight margins. In these features the jaw of this whale is distinctly more like that of *Rhachianectes* than of any other Whalebone Whale[1]. Restricting our comparison to the genera *Balæna* and *Balænoptera*, it is clear that *Neobalæna* in the characters of the lower jaw comes nearest to *Balæna*. This it approaches in two marked features: in the first place, it agrees with *Balæna* in the feeble development of the coronoid process; and in the second place, of the downward inclination of the symphysial region of the bones. It is, however, proportionately much deeper than in *Balæna*. This latter statement also applies to a comparison of it with *Balænoptera*. As in other Whalebone Whales, the angle of the lower jaw does not project back beyond the condyle.

It will be apparent from the above description of the skull of *Neobalæna* that it most resembles that of *Balæna*, but that it shows a few points of approximation to the skull of *Balænoptera*, and possesses a few others in which it is peculiar and unlike either genus.

I propose on a future occasion to compare the skull and the skeleton of *Neobalæna* with that of another aberrant Whalebone Whale, *Rhachianectes*. But, in the meantime, I may point out that the two genera seem to have pursued two different paths of modification. While *Neobalæna* may be best described, perhaps, as a Right Whale with a dash of Rorqual about it, *Rhachianectes* is decidedly a Rorqual with about an equal mixture of Right Whale.

It may be useful to abstract from the foregoing account of the osteology of *Neobalæna marginata* the features in which it presents resemblances to the genera *Balænoptera* and *Balæna* and to contrast with these the peculiarities which appear to be distinctive of the genus *Neobalæna*.

Neobalæna agrees with *Balæna* in the following assemblage of characters:—

(1) The arching and the narrowness of the anterior part of the skull.
(2) The absence of a marked coronary process upon the mandible.
(3) The complete fusion of the seven cervical vertebræ.
(4) The great length and the characters generally of the whalebone.
(5) The absence of throat-grooves.

Neobalæna agrees with the genus *Balænoptera* in the following larger number of characters:—

(1) The proportions of the skull to the rest of the skeleton.
(2) The great breadth and the shortness (from above downwards) of the orbital portion of the frontal bones.
(3) The small number of ribs which possess the capitular head.
(4) The general shape of the scapula.

[1] It should be noted that in the drawing which illustrates the dorsal view of the mandibles (Pl. VIII. fig. 1) those bones are a little displaced, and thus appear to contradict the above statements.

(5) The proportions of the arm to the forearm.
(6) The existence of only four fingers in the manus [1].
(7) The presence of a dorsal fin.

The anatomical features in which *Neobalæna* is peculiar and disagrees with both Right Whales and Rorquals are more numerous still; they are as follows:—

(1) Small size (*cf.*, however, *Balænoptera rostrata*).
(2) The great length of the region of the skull which lies behind the orbit.
(3) The depth and the form generally of the mandibles.
(4) The large quadrangular lower transverse processes of the cervical vertebræ.
(5) The great shortness of the entire vertebral column.
(6) The extremely reduced lumbar region of the vertebral column.
(7) The large number of the ribs, their breadth and flatness, and the commencement of the series with the second and not the first dorsal vertebra.
(8) The shape of the sternum.

From these facts a definition of the genus may be compiled, and will be the following:—

Genus Neobalæna.—Size small, 20 feet or so. Dorsal fin present. No throat-grooves. Head hardly more than one-fifth of the length of the entire body. Baleen long. Skull like that of *Balæna*, but with much produced postorbital region and broader frontals. Mandible deep, with only a rudimentary coronoid process. Cervical vertebræ completely fused, the lower transverse processes forming a strong quadrangular mass. Dorsals 18 in number. Lumbars 2. Caudals 16. Ribs very numerous, 17 pairs, the first attached to the second dorsal vertebra; the posterior ribs broad and flattened, the first six only with traces of capitulum. Shoulder-girdle elongated antero-posteriorly, with long coracoid and acromion. Head shorter than radius. Digits four. Sternum cross-shaped.

P.S., *May* 1901.—Since this paper was read, Mr. S. F. Harmer, F.R.S., has kindly directed my attention to a skeleton of *Neobalæna marginata* in the Museum at Cambridge. In this example, which is immature, the epiphyses of the vertebræ being quite separable, the sternum has an outline different from both the two examples with which I have dealt above. In the Cambridge specimen the outline is roughly that of a half an oval divided across the longer diameter. The straight edge forms the anterior border.

There are seventeen ribs on each side, and to the first dorsal vertebra no rib is

[1] I am, of course, aware that Dr. Kükenthal ("Die Walthiere," in Denkschr. Jen. Ges. 1889) has shown that in *Balænoptera musculus* there are a series of cartilaginous pieces intercalated between the third and fourth fingers, which he considers to represent the missing digit of the adult Rorqual hand. If this be shown to be a general feature, it will not interfere with the anatomical difference between *Balæna* and *Balænoptera* in the manus, though it will, of course, show that the supposed thumb is not the equivalent of that digit.

attached. It is highly improbable, Mr. Harmer informs me, that it ever had a pair of ribs.

The first five cervical vertebræ are completely fused, except, of course, for the nerve-foramina. The neural arches of the 6th and 7th vertebræ are free from the others, except mid-dorsally and for a short distance on each side of the middle line. The 6th and 7th vertebræ are also partly free from each other in their centra. On the right side of the body there is a similar slit dividing the 5th from the 6th vertebra.

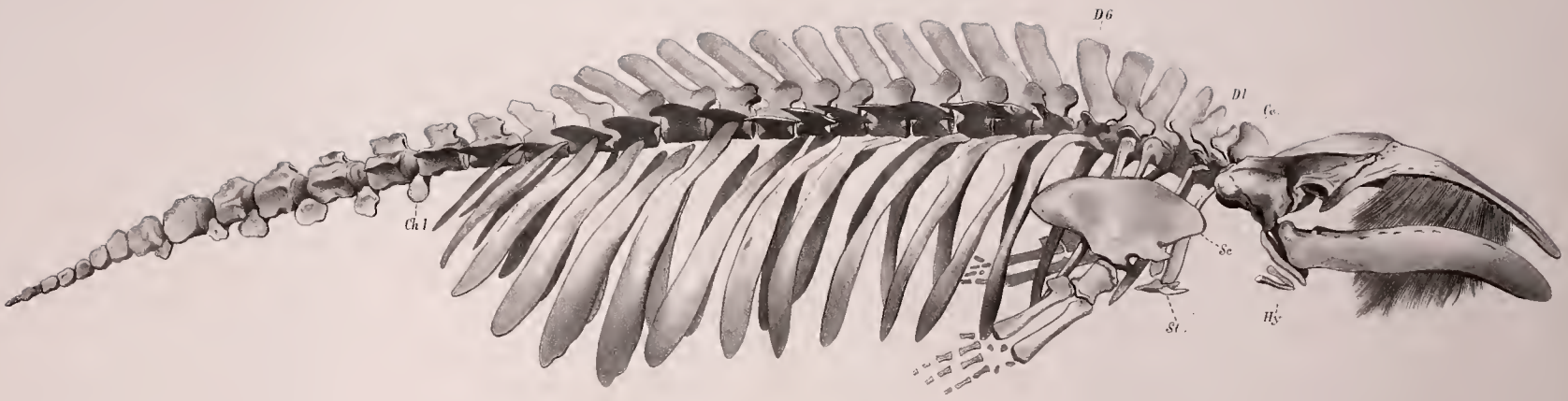
I have to thank Mr. Harmer for this information.

PLATE VII.

EXPLANATION OF THE PLATES.

PLATE VII.

Skeleton of *Neobalæna marginata*, one-tenth natural size. From an adult specimen mounted in the Whale Gallery of the Natural History Museum, South Kensington. *D.i.*, first dorsal vertebra; *D.* 6, sixth dorsal vertebra; *Ce.*, mass of cervical vertebræ; *Ch.i.*, first chevron-bone; *Hy.*, hyoid; *Sc.*, scapula; *St.*, sternum.



W.S Berridge del J Smit lith.

OSTEOLOGY OF NEOBALÆNA MARGINATA.

Mintorn Bros imp

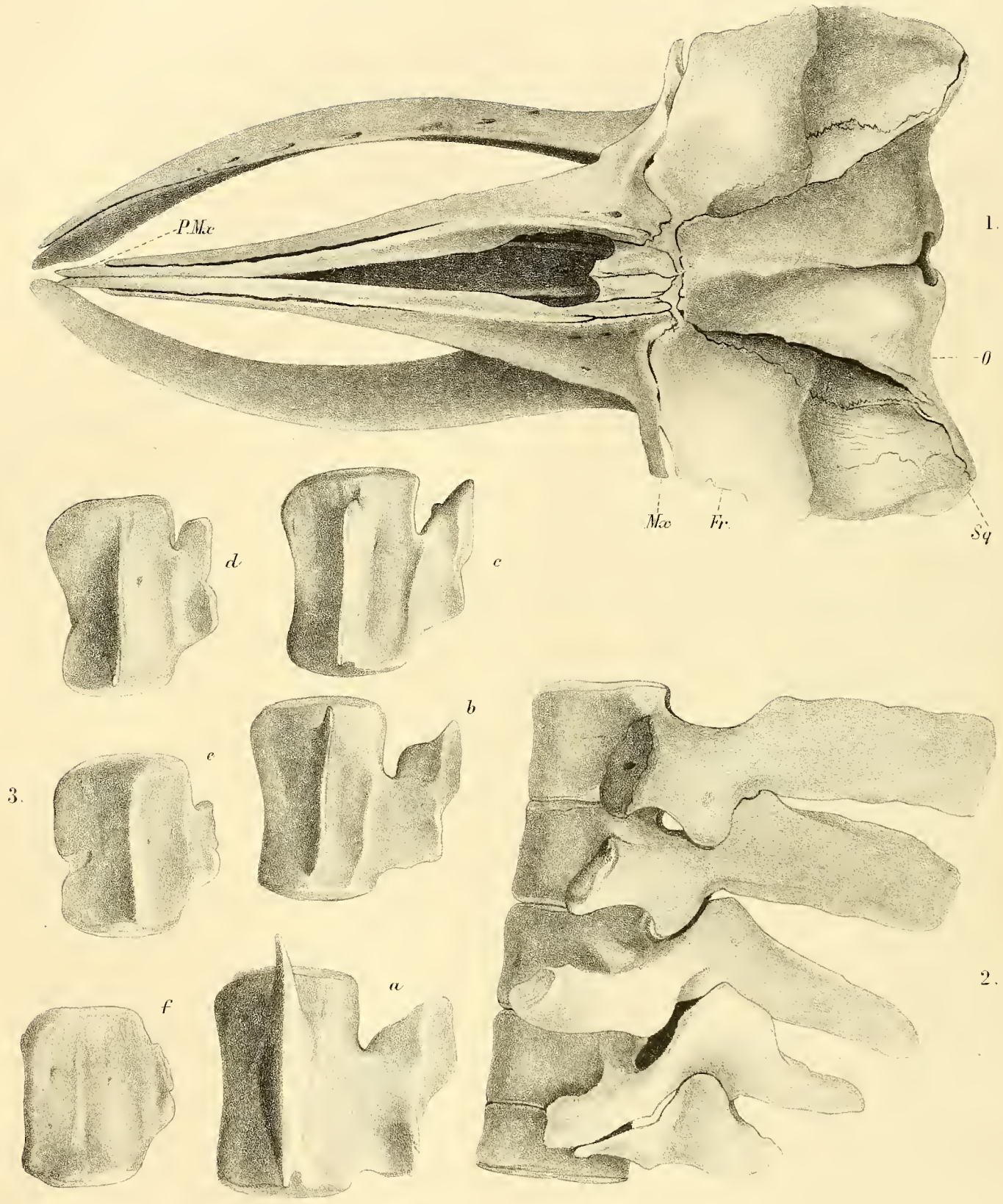
PLATE VIII.

PLATE VIII.

Fig. 1. Skull of *Neobalæna marginata*, viewed from above. *Fr.*, frontal bone; *O.*, occipital; *Mx.*, maxilla; *P.Mx.*, premaxilla; *Sq.*, squamosal.

Fig. 2. First four dorsal vertebræ of the same.

Fig. 3. First six caudal vertebræ of the same: *a*, the first vertebra; *b*, the second, &c.



W.S.Berridge del. J.Smit lith.

Mintern Bros imp.

OSTEOLOGY OF NEOBALÆNA MARGINATA.

PLATE IX.

PLATE IX.

Fig. 1. Skull of *Neobalæna marginata*, lateral view. *C.*, coronoid process of mandible; *Fr.*, frontal bone; *L.*, lacrymal; *Mx.*, maxilla; *O.*, occipital; *Sq.*, squamosal.

Fig. 2. Sternum. The figure is drawn a little in profile, as it was impossible to get an accurate view of this bone from above.

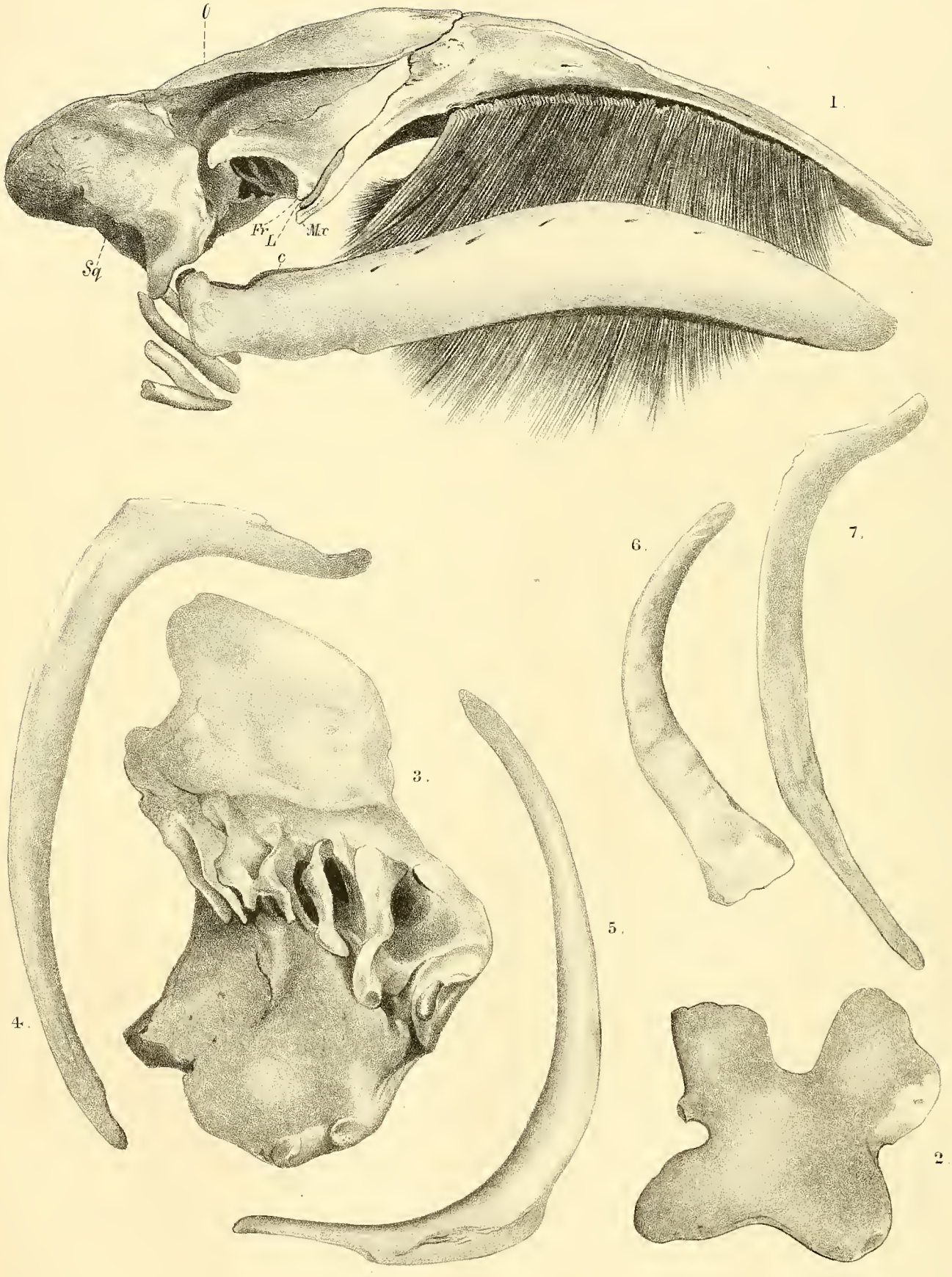
Fig. 3. Cervical vertebræ.

Fig. 4. Third rib.

Fig. 5. Fourth rib.

Fig. 6. First rib.

Fig. 7. Fifth rib.



W. S. Berridge del. J. Smit lith.

OSTEOLOGY OF NEOBALÆNA MARGINATA.

Mintern Bros. imp.

III. *On the Breeding-habits of some West-African Fishes, with an Account of the External Features in Development of* Protopterus annectens, *and a Description of the Larva of* Polypterus lapradei. *By* J. S. Budgett, *M.A., F.Z.S., Trinity College, Cambridge.*

Received and read December 4, 1900.

[Plates X. & XI. and text-figures 19–23.]

Contents.

	Page
I. Introduction	115
II. Results of the Search for *Polypterus* Eggs	116
III. The Habits and Life-history of *Protopterus*	119
a. Nesting-habits.	
b. Development of the Embryo.	
IV. The Nesting-habits of *Gymnarchus*	126
V. The Nesting-habits of *Heterotis niloticus*	128
VI. The Nesting-habits of *Sarcodaces odoë*	130
VII. The Nesting-habits of *Hyperopisus bebe*	130
VIII. Conclusion	131
IX. Explanation of the Plates	132

I.—Introduction.

THE months of June, July, and August of this year I spent on M'Carthy Island, in the river Gambia, hunting for the eggs of *Polypterus*. But in this paper I have recorded not only the result of my work in this direction, but also my observations upon the breeding-habits of the African Lung-fish, *Protopterus annectens*, of the Teleosteans *Gymnarchus niloticus*, *Heterotis niloticus*, and *Sarcodaces odoë*, and also my observations upon the nests of another Teleostean, presumably *Hyperopisus bebe*. Towards the expenses of this expedition I received contributions from the Government Grant, from this Society, and from the Cambridge University Balfour Fund. I should here like to express my gratefulness for this assistance, which enabled me to undertake what turned out to be, so far as I was concerned, an intensely interesting collecting trip. When my results are completed, the expenditure will, I hope, be found to have been justified.

The Island of M'Carthy is six miles long and about one mile wide, and is situated 160 miles up the river Gambia. The whole of the island is low-lying, and the greater

part, in the wet season, is completely under water. On the highest part of the island is the native town of Ginginberri, and the ruins of the old military settlement where I lived. The eastern half of the island is partly under cultivation, and here the natives plant rice on the low land, and kuskus or millet on the high land. The western half of the island is little cultivated, and here was my hunting-ground.

The whole island is traversed by one main swamp, which has the appearance of having been at one time an old bed of the river, and which is seldom quite dry, even in the dry season. Parallel with this lie several shallower and more irregular swamps, all of which become perfectly dry in the dry season. These swamps are separated by belts of low forest, composed largely of leguminous trees, palms, and fig-trees. The swamps themselves are mostly choked with papyrus and other swamp-grasses; while in the middle there is often a little open water covered with several kinds of lovely water-lilies.

The amount of open water depends largely on the rapidity of the oncoming of the rains. In the present season there was little open water, as the rains came on very slowly and gave the grass time to grow abundantly.

As the rainy season advances the swamps become filled with water, the river rises and soon becomes connected with the swamps by narrow creeks, up which great numbers of fishes pass to the flooded grasslands to spawn. Conspicuous amongst these are the two species of *Polypterus*—*P. lapradei* Steind. and *P. senegalus* Cuv.

II.—Results of the Search for *Polypterus* Eggs.

From what I observed in my former expedition of its habits, I concluded that the eggs of *Polypterus* might be obtained by one of three methods:—

(1) Hunting the flooded grasslands for the eggs in a state of nature.

(2) Inducing *Polypterus* to breed in captivity.

(3) Artificially fertilizing the eggs of the female.

The first method was persistently tried without success, especially on the occasion of spawning females being brought in, when, taking a number of natives to the spot, we examined every foot of water within a hundred yards of the place where the female had been caught. Five spawning females were caught, but in no case did I find a single egg.

For the purpose of the second method I took out to the Gambia with me a large number of wire hurdles, with which I made four enclosures in the swamp. During the second half of June about fifty *Polypteri* were caught in pools by the river-side. As the rains had scarcely begun, and consequently there was no water as yet on the land where I had made my enclosures, I temporarily turned my fish into large floating cages in the river, and fed them regularly on minced meat. A few days after turning them in, I came one evening to feed them, and found that the two cages

had been torn to pieces by crocodiles and the fishes had escaped. I then rigged up some temporary cages in pools by the river-side, into which I turned six pairs of *P. lapradei* and fifteen pairs of *P. senegalus*. By the 30th of July there was sufficient water in my swamp-enclosures to turn in the fishes, and there they seemed quite happy, as the grass was now two feet high and I fed them regularly every night. The enclosures were each eighteen feet long and six feet wide. As soon as I put the food into the water at one end of the enclosure the *P. senegali* came hurrying through the grass from all parts, and greedily devoured it without the least appearance of shyness. The *P. lapradei*, however, were considerably more shy, and continually damaged themselves against the wire netting. Thus the *Polypteri* remained until the 5th of September, and though I examined every inch of the enclosure every other day, I found no traces of eggs.

The third method was not tried so frequently as I could have wished, as I could not obtain anything like the number of *Polypteri* that I procured in the previous season. The natives at this time use a kind of basket for catching fishes, which is called the "wusungu." This they deftly drop over the fishes as they see them move in the grasses, and putting their hand into the basket from above, draw forth the captives. Whereas by this method I obtained an abundant supply of *Polypterus* last year at the price of sixpence apiece, this year I raised the price to two shillings apiece and was yet unable to get any large number of specimens.

The first spawning female was brought to me on the 3rd of July. It was a *Polypterus senegalus*, and, on holding it up by the head, it extruded successively twelve eggs. I had two males with which I tried to fertilize these eggs. One by one I tried them: first by placing them on the anal fin and on the vent of the male, then by mixing them with the fluid obtained from the seminal duct, and lastly by mixing them with fluid obtained from the minced testis. These eggs were then transferred to muslin stretched on a frame and placed in a large quantity of river-water. They soon attached themselves to the muslin, but though I watched them until late into the night, no further change took place and they one by one decomposed. On cutting open the female I found to my disappointment that there were no free eggs in the body-cavity, but that they were all attached to the ovary by their follicles.

The next spawning female was obtained on July 19th, when a fisherman brought me a female *Polypterus lapradei* which had two eggs in the oviduct and practically none in the ovary. There were no free eggs in the body-cavity.

On August the 9th a female *P. lapradei* was brought which had evidently spawned some time ago.

On August the 14th a female was brought which had nearly finished spawning. There were, however, no free eggs in the body-cavity. I tried to force out the eggs from the ovary, and in this manner several came away fairly easily, and I made every effort to fertilize them, but again without success.

On August the 15th another female *Polypterus* was brought, which had shed all its eggs.

In each case I took several natives to the spot where the female had been caught and made a very thorough search for the eggs in the neighbourhood, examining every blade of grass, but found not a single egg.

On August the 19th a small boy brought me a specimen of *Polypterus lapradei* only one inch and a quarter in length; it was a most beautiful object (Pl. XI. fig. 1). The upper surface is marked with black stripes on a golden ground, a conspicuous golden stripe runs on each side above the eye, across the spiracle, and along the dorsal surface of the external gill [1]. The external gills are at this stage of great size, reaching halfway to the tail, blood-red, and with a row of branches on either side. Each branch bears a row of pinnules on either side; the pinnules have the same structure as those of most Amphibian and Dipnoan external gill-filaments, being merely a long drawn-out blood-capillary loop. The afferent limb of the loop arises from the afferent artery of the gill-branch; the efferent limb of the loop joins the efferent artery of the gill-branch. Similarly the afferent artery of the gill-branch arises from the afferent artery of the external gill, while the efferent artery of the gill-branch joins the efferent artery of the external gill. Every alternate gill-branch is much smaller than the next gill-branch (Pl. XI. fig. 2). Each of these small gill-branches bends towards the surface of the body, while the large gill-branches extend parallel with the body. Thus space is economised, and the result is the same as four rows of branches on the external gill. Arising immediately behind the spiracle, the external gills may droop ventralwards posteriorly, and do not seem to be moved much by muscles, except just to straighten the shaft from the drooping position. The heart and blood-supply to the external gills can be seen with wonderful distinctness through the transparent ventral body-wall. The dorsal finlets are not differentiated from the tail, of which they seem to be only a forward prolongation. They are not distinct from one another, but form rather a continuous dorsal fin. The body is distinctly more truncate in the larva than in the adult, the head and tail-region being large. The eye is also very large in proportion.

The area of pigment ceases abruptly ventralwards in a line running from the tubular nasal opening under the eye dorsal to the shaft of the pectoral fin, thence to the base of the anal fin.

The larva was extraordinarily active, and, during the moments when it was at rest, supported the weight of its body on its pectoral fins, the blade of the fin being turned forwards and not backwards as is usually the case in the adult. The shape of the pectoral fin differs considerably from that of the adult. The ventral or postaxial border

[1] The young larva which I have described is about one third of the length of any larval Crossopterygian which has, up to the present time, been obtained. The anatomy of this specimen I hope to describe in a future paper.

of the basal lobe is in this young larva much longer than the dorsal or preaxial border; while the fin-rays become successively longer in passing from the preaxial to the postaxial border. It follows that the shape of the fin is triangular, the apex being at the extremity of the postaxial border (Pl. XI. fig. 1).

Though the spot where this larva was caught was carefully searched, I did not succeed in capturing another.

Later on the same day, the 19th of August, I had another female *P. lapradei*, which must have finished laying its eggs some weeks before.

On the 21st of August, in my own fish-trap at the mouth of the small creek which led from the river to the swamp, I found a female *P. lapradei* which had finished laying its eggs, and it looked as though, in this case, it had spawned in the river or else at the mouth of the creek. I am inclined to believe, however, that it had temporarily returned to the river side of the trap after depositing its eggs in the swamp.

On this same day I had a *Polypterus senegalus*, still crammed with eggs, but not one free egg in the body-cavity.

During the last week in August and the first in September, I killed fifteen of my captive females; but in no case could I attempt artificial fertilization, as the ova would not come away from the ovaries, and in more than one case there were signs of degeneration.

On the 5th of September I left for England, leaving five pairs of *P. senegalus* in charge of a native, who was to preserve eggs for me if any should be laid.

Though I have little success in this direction to report, I have thought it well to put on record the difficulties which I encountered in the search for the eggs of *Polypterus* in order that any future investigator who may attempt to obtain developmental material of this fish may in being forewarned be also forearmed.

The main difficulties in obtaining the eggs seem to lie in the fact that *Polypterus* probably makes no nest, and certainly lays but few eggs at a time, these being scattered, probably broadcast, throughout the thick vegetation of the flooded grass-lands. The eggs are minute, and therefore the chances of finding them in a state of nature are small in the extreme.

III.—The Habits and Life-history of *Protopterus*.

a. *Nesting-habits.*

Although the development of *Polypterus* had been the chief aim and object of my second journey to the Gambia, I was also very anxious to obtain a series of the eggs and embryos of *Protopterus*. When I was on the Gambia the previous year, I had brought me a number of eggs of *Protopterus*, but I suspected that the way in which the native told me that they had been laid was quite abnormal or altogether untrue.

I had expected, in wading about the swamps, to come across deep holes in the ground similar to the nests of *Lepidosiren*, which I had become familiar with when in the

Gran Chaco of Paraguay some three years ago with Mr. Graham Kerr. However, I never found such holes, and was completely at a loss to know where to look for the nests of *Protopterus*, the natives being entirely ignorant of any but the most obvious facts of natural history, and having declared to me that the "Cambona," as they called *Protopterus*, was viviparous.

One day my head fisherman, Sory, came to me in a great state of excitement to say that he had found the children of the Cambona. It was scorching mid-day in the height of the rainy season, the temperature 99° in the shade. After crossing one deep swamp we came to the edge of another swamp, and there, about ten yards from the water's edge, on dry ground, was an oval-shaped hole filled with water, and in the water was a great commotion (text-fig. 19); the surface of the water was being continually lashed from side to side by the tail of a Cambona, the head of which was away down under the ground. On being startled, the Cambona disappeared downwards, and the fisherman, putting his hand into the hole, drew forth a handful of larval *Protopteri*.

Text-fig. 19.

Nest of *Protopterus*.

Having now learned where to look for the nests of *Protopterus*, in a few days I found a number of similar nests, but never so far away from the water as the first one, which was found at the end of a period of drought, very unusual at this time of year. I soon found a nest full of newly-laid eggs which must have numbered several thousands, for from the first day to the day the larvæ left the nest, twenty days later, I took fifty per day for preservation without perceptibly diminishing the numbers in the nest.

Throughout the period of the larvæ being in the nest, the male *Protopterus* stays with them and guards them jealously, severely biting the incautious intruder. On one occasion the male was observed to leave the nest and to come out by a small opening which had hitherto been unnoticed, and wriggle off down to the water. This exit was always found about two feet from the main opening. Frequently there was a kind of pathway up to the entrance, where the grasses were bent aside. The main opening measured four to ten inches in diameter, while the exit rarely measured more than three inches. The depth of the nest was usually about a foot, and the shape of the nest was quite irregular. There was never any lining, and the eggs were laid on bare mud. All the males found in the nests measured about eighteen inches in length.

b. *Development of the Embryo.*

The eggs, which measure 3·5–4 mm. in diameter, begin to hatch about the eighth day, and by the tenth day the larvæ are all attached by their suckers to the side of the nest. The main features in development are remarkably like those of *Lepidosiren* lately described by Kerr, the larvæ being provided with a ventral sucker and four pairs of plumose external gills, one to each branchial arch. I have figured a few stages of the external features in development, most of which were drawn on the spot from life, in order that a comparison may be made with Kerr's excellent illustrations in the Phil. Trans. vol. 192, plates 8–12.

As all my specimens were procured from the same nest at twenty-four hours' interval, I am able to show the advancement made daily. As Kerr's material was obtained from a large number of nests, he was unable to say what was the age of each successive stage figured. Though in one nest were found a few specimens at least half a day in advancement of the rest, and a few also at least half a day behind the rest, yet the majority appeared to be at a uniform stage of development. When kept in shallow dishes I found that the development was much retarded.

Comparing Pl. X. fig. 1 with the corresponding stage in *Lepidosiren* (*op. cit.* plate 8. fig. 7*a*, 7*s*, & 7*b*), it is noteworthy that the egg is here divided into segments, which are more distinct from one another, the outer surfaces being rounder and not assuming the same curvature as the egg-capsule. In this the egg of *Protopterus* approaches the conditions of *Ceratodus*. This is the first stage of my series, so that I am not able to speak with regard to the appearance of the egg in the earliest stage of segmentation.

The subsequent down-growth of the epiblast over the invaginating yolk (as shown in Pl. X. figs. 2, 3, 4, & 5) is remarkably similar to the same process in *Lepidosiren* (*op. cit.* plate 8. figs. 10–14), the invaginating rim remaining a nearly straight line. This appears to me to be the more frequent method of invagination. Mr. Kerr has himself, however, pointed out to me that the variations which frequently occur in

Protopterus are very interesting. The invaginating rim is often curved, as in fig. 3 *a*, rather than straight, as in fig. 3, while later the invaginating rim may become somewhat V-shaped, recalling a similar appearance in certain Amphibia. The invagination culminates in a crescentic blastopore. The yolk from the earliest stage onwards in *Protopterus* is light green in colour. During segmentation the epiblastic pole of the egg is pink, and this colour gradually replaces the green colour of the yolk, becoming, however, paler as invagination proceeds. In the later stages, where the tissues are becoming more transparent, the green-coloured yolk is again seen.

As in *Lepidosiren*, the medullary groove arises far forwards and grows back to the blastopore. In *Protopterus* (Pl. X. fig. 6) the medullary folds, though wider in proportion to the surface of the egg than in *Lepidosiren* (*op. cit.* figs. 17 *h* & 18 *h*), are not quite so definite, but undoubtedly do encircle the blastopore in the same way just before they close. From an external examination the blastopore seems to remain more widely open after closure of the medullary folds than in *Lepidosiren*.

Pl. X. figs. 7 & 8, corresponding with *Lepidosiren* (*op. cit.* figs. 21, 22, & 23), show a very similar origin of the brain, optic outgrowths, branchial and pronephric eminences, but the pair of folds which will subsequently give rise to the mandibular and hyoidean visceral arches is much more marked in *Protopterus* (Pl. X. fig. 7, *M.H.*). The pronephric ducts have also an origin identical with *Lepidosiren* (*op. cit.* figs. 21 *m*, 22 *m*, 23 *m*). In Pl. X. fig. 8, which corresponds very nearly otherwise in development with *Lepidosiren* (*op. cit.* fig. 23 *l*), the whole embryo is not so flattened on the yolk, the head and tail-fold being much more conspicuous. At this stage is seen the first appearance of the crescent-shaped sucker (Pl. X. fig. 8, *c.o.*) first shown in *Lepidosiren* (*op. cit.* fig. 24).

In *Lepidosiren* the branchial arches arise on either side, first as one eminence (*op. cit.* fig. 22), later three eminences (fig. 23); the last of these then splits into two, and thus the four arches are formed. In *Protopterus* they arise first as one eminence (Pl. X. fig. 7, *br.*); later two eminences (Pl. X. fig. 8, *br.* I. & II., *br.* III. & IV.), these then each split into two[1] (Pl. X. fig. 9, *br.* I. II. III. IV.), thus giving rise to the four branchial arches.

In *Protopterus* (Pl. X. fig. 9, *M.H.*), anterior to the four branchial arches, there may be seen an indication of the mandibular and hyoidean arches, which in *Lepidosiren* (*op. cit.* fig. 24) are represented by a single eminence.

Protopterus hatches about the stage of Pl. X. fig. 10, often a little later, in some cases as late as Pl. X. fig. 11. Before hatching there appears to be a covering of cilia, for particles in the fluid within the egg-capsule stream down the sides of the embryo towards the tail end. At hatching the four pairs of external gills are a good deal in advance of the gills of *Lepidosiren*, the developing pinnæ being clearly seen. The rate and direction of growth of the first pair of external gills is very different to that of

[1] The cleavage of the hindermost eminence to form the 3rd and 4th branchial arches occurs somewhat later than that of the foremost eminence.

the succeeding pairs as shown in Pl. X. figs. 10 & 11, *Eg.* 1. Here also may be seen, through the dorsal wall, the auditory cavities and the now large fourth ventricle.

Just before the stage of Pl. X. fig. 12 is reached, pigment begins to appear first in the retina, then on the surface of the head. The fin-folds of the tail now begin to grow rapidly, and attain a much greater size than in *Lepidosiren* (*op. cit.* figs. 31, 32, & 33). A copious network of blood-vessels spreads over the yolk. The sucker is fully functional, and the larvæ hang vertically from the sides of the nest or vessel in which they may be confined. Although in *Lepidosiren* this organ is more conspicuous, yet the larvæ appear only to use it for clinging to the uppermost layer of débris in the nest, and so prevent their falling downwards and getting smothered [1].

A striking feature of *Protopterus* at this stage, compared with *Lepidosiren* (*op. cit.* figs. 31, 32), is the serial arrangement of the external gills, their roots being distinct from one another, and placed in a line along the dorsal surface of the deepest part of the yolk. Anterior to the first branchial cleft there is a faint indication of a spiracular cleft between the mandibular and the hyoidean arches (Pl. X. fig. 12, *sp.*) of which in *Lepidosiren*, externally at least, there is no trace.

The roots of the external gills in *Protopterus* (Pl. X. fig. 13) remain longer separated from one another than in the *Lepidosiren* (*op. cit.* fig. 33). The three posterior pairs also attain a greater proportionate size. At this stage the tail and dorsal fin-fold are considerably more developed than in the corresponding stage of *Lepidosiren*.

As the external gills are reaching their maximum development, the origin of the gills become somewhat concentrated and rotate forwards, the hindermost gill becoming dorsal, the anterior becoming ventral.

For some days before leaving the nest, when the young larvæ are hanging suspended vertically from its walls by their suckers, the external gills are held stiffly out at right angles to the axis of the body, forming a radiating frill around the base of the head. When the larva is lying in a small trough of water, the gills are not thus erected, and as the drawing (Pl. X. fig. 13) was taken from a living specimen, the gills are shown lying back along the sides of the body.

The pectoral and pelvic limbs develop synchronously as in *Lepidosiren*, and are just beginning to bud in Pl. X. fig. 12, *h.l.* Correlated with the extension backwards of the roots of the external gills, the position of the bud of the pectoral fin is also far back, and lying immediately below the last external gill, is hidden by them. In Pl. X. fig. 13 the pectoral limbs are of about the same size as the shafts of the external gills. In one case a specimen had not developed the pinnæ of one external gill. This bare shaft so much resembled the pectoral limb, that the larva appeared to have two pectoral limbs on one side.

In Pl. X. fig. 13 the operculum is growing back, the mouth is open, and the internal gills functional. The larvæ do not breathe air before leaving the nest. There is now a considerable development of pigment, especially in the anterior dorsal part of the

[1] Kerr, *loc. cit.* p. 316.

body. The fin-rays are just making their appearance in the fin-folds of the tail. The sucker or cement-organ is at its maximum development. The tail is absolutely diphycercal from the first. Blood-vessels running in the track of the spiral valve shine through the body-wall (Pl. X. fig. 12, *s.v.g.*). The spiral valve is first indicated in fig. 12. The yolk remains chiefly massed in the original position close behind the sucker, and is not distributed along the gut to the same extent as in *Lepidosiren* (*op. cit.* figs. 33, 34, & 35). Wherever yolk is seen, it is of the original greenish colour.

The young *Protopterus* leaves the nest with practically the form of the adult (Pl. XI. fig. 3). The mass of food-yolk is not entirely absorbed as yet. The first pair of external gills has been lost, and the succeeding pairs have been much reduced in size. The tail ends in a very fine filament. The markings of the young *Protopterus* at this time are somewhat different from the adult. The general colour is dark brown, a conspicuous broad yellow band passing between the eyes. As with *Lepidosiren* so with *Protopterus*, the larvæ at this stage contract their black chromatophores at night and become blood-red, the eye shining out deep black in contrast.

It is here interesting to notice that the larval *Protopteri*, after leaving the nest when kept in an aquarium the bottom of which was covered with seedling water-lilies, chara, &c., never show themselves by day, and if disturbed from their seclusion, hastily make their way back to their hiding-place. After dark, however, by the aid of a lantern, the larvæ may be seen swimming around in the most lively manner, but they do not come to the surface for air.

It seems, then, that the habit of expanding the chromatophores by day is of advantage to the larval *Protopterus*, making it almost invisible while lying passively on the dark soil. The chromatophores become contracted by night, not by reason of the darkness, but because this is the period of activity with the larvæ, and when swimming about they are certainly less conspicuous when transparent than when opaque, even at night.

Were it customary for the larval *Protopterus* to swim about in the daytime, they would probably then contract their chromatophores, becoming less visible with increased transparency. As a matter of fact, when in the daylight the larvæ were placed in a white porcelain dish, in a large number of cases they did contract their chromatophores. That this contraction on a light background did not always take place may possibly be accounted for by supposing that continued habit has produced a certain periodicity in the contraction and expansion of the chromatophores.

While on the Gambia, I kept a large number of young fry of about fifteen species of fishes, and I noticed that the nocturnal forms did become more transparent at night. The converse was naturally not noticed, since I know of no fishes which are only active in the daytime. With frogs, the case is quite different, for they are not aquatic, and would not therefore be made less conspicuous by being transparent. The chromatophores are often contracted by them in the daytime when exposed to strong sunlight, for the objects around them then become of brighter and lighter colour [1].

[1] "Notes on the Batrachians of the Paraguayan Chaco," Q. J. M. S. 1899, pp. 314, 327, 328.

Soon after leaving the nest, the larvæ begin to feed on almost any animal matter they can get. For this reason, though I started homewards with a number of larvæ taken from the nest, only one reached England alive, having eaten all the others. On the voyage home, the young *Protopterus* began to move about in the daytime, ceased becoming transparent at night, lost the external gills, all but small vestiges, and began to come to the surface for air. This was about one month after leaving the nest, or about seven weeks after being laid. On reaching England it had quite the form of the adult.

In comparing the development of *Protopterus* with that of *Lepidosiren*, a very noticeable circumstance is the impossibility of comparing together a larva of each form as being exactly at the same stage of development. The various organs and features do not make their appearance in quite the same proportionate periods of time in the two forms; so that at any one stage, some set of organs in the one will not correspond in its state of development with the same set in the other.

Many of the differences noted in the external development of the two forms may, I think, be correlated with the presence in *Lepidosiren* of rather more food-yolk. The main differences are:—

1. A more complete separation in *Protopterus* of the cleavage-products.
2. The greater size of the medullary folds.
3. A more distinct remnant of the blastopore.
4. The earlier appearance of the cement-organ.
5. The earlier rising-up of the embryo off the yolk.
6. The appearance of two visceral folds in front of the four branchial folds.
7. A rudiment of a cleft between them.
8. The greater size of the gills at hatching.
9. The more complete separation of the external gills.
10. The rotation forwards of the external gills.
11. The concentration of the yolk forwards.

I have not thought it well to make any observations upon the bearings of the facts here described, since it is first necessary to know more of the development than can be learnt from a superficial examination. Mr. Graham Kerr has undertaken to further study the development of *Protopterus* and to incorporate the results in his work on the development of *Lepidosiren*. I have here described the external features in development together with what I observed of the nesting-habits of *Protopterus*, as it would be difficult to treat either separately.

Comparing the nesting-habits of *Protopterus* with those of *Lepidosiren*, perhaps the most striking difference is the development by the male *Lepidosiren* in the breeding-season of the extraordinary vascular fringes of the pelvic fins, recently described by Kerr. Nothing of the kind is developed by *Protopterus*. Now, looking to the solution

of the problem as to what is the function of these fringes in *Lepidosiren*, it is natural to look to see in what the habits of the latter differ from those of *Protopterus*.

The most striking difference is surely that, whereas *Lepidosiren* makes its nest several feet below the surface of the water, *Protopterus* makes its nest practically out of the water. I regard the habit of *Protopterus* of lashing the surface of the water at the entrance to its nest as a means of aerating the eggs in the nest. Now, it is tempting to regard the vascular fringes on the pelvic limbs of *Lepidosiren* as in some way connected with the aeration of the eggs, for it is obviously unable to make use of this method of aeration adopted by *Protopterus*. But the conditions under which this habit was observed in *Protopterus* were, as I have said, somewhat unusual, in that, owing to prolonged drought, the water in the nest was unconnected with the surrounding water. When this was not the case, the lashing of the tail on the surface of the water was not observed. Therefore I do not think this habit can be said to be quite characteristic of *Protopterus*. The entrances to the nests, however, were always only a few inches at most below the surface of the water, while with *Lepidosiren* the nests are made in deep water, and it seems more probable that the fringes on the pelvic limbs of *Lepidosiren* are, as Kerr holds, accessory organs of respiration avoiding the necessity of frequent absence from the nest in order to visit the surface for air, and thus perhaps risking loss of the entrance to the nest or the attacks of enemies. *Protopterus*, by reason of the shallowness of the water about the entrance to the nest, would not run these risks in seeking air, and therefore has no need of the accessory breathing-apparatus.

IV.—The Nesting-habits of *Gymnarchus*.

While hunting for *Polypterus* eggs, I met with several large floating nests measuring in all two feet in length and one in breadth. The nests were made in the dense grasses of the swamp in three to four feet of water (text-fig. 20). The inside measurement was about a foot by six inches. Three sides of the nest projected from the water; the fourth side was several inches lower, being about two inches below surface. The deepest part of the nest was opposite to that side where the wall was low, the bottom being about six inches below the surface of the water.

In this nest were deposited about a thousand large spherical amber-like eggs 10 mm. in diameter. The eggs hatched five days after being laid, and in eighteen days a thousand young fry of *Gymnarchus niloticus* left the nest when three inches long. This fish is called by the natives the "Suyo."

Though there are many interesting features in the development of these eggs, I do not intend to deal with them in detail here, but merely to mention that the development is exceedingly shark-like. The larvæ soon after hatching develop extremely long gill-filaments, which hang down in two blood-red branches from the gill-arches, of which there are four. The yolk-sac, at first spherical, later becomes drawn out into a

long cylindrical bag, attached somewhat far behind for a Teleostean, and covered with a vascular network (Pl. XI. figs. 4 & 5).

The tail is from first to last perfectly diphycercal, and is at first provided with a dorsal and a ventral fin-fold reaching right to the tip of the tail.

Before leaving the nest, both outer gill-filaments and yolk-sac are absorbed and the mature form is reached.

Immediately after hatching, the larvæ commence their characteristic movements, throwing the head and fore part of the body from side to side incessantly. The larvæ are at first so small in proportion to the size of the yolk-sac, that they are quite unable to move it. By this constant movement the larvæ tend towards the surface, and the

Text-fig. 20.

Floating nest of *Gymnarchus*.

weight of the yolk tending downwards, the yolk-sac becomes gradually drawn out into the long appendage already mentioned. About three days after hatching, the larvæ are strong enough by their movements to raise the yolk-sac off the bottom of the nest for a moment, but it is quickly drawn back by its weight.

By the tenth day after hatching, the larvæ are able to drag their yolk-sac to the surface of the water, when they take a gulp of air into their lung-like swim-bladder and fall again to the bottom, on reaching which they again start for the surface with unceasing regularity, so that when looked at from above the nest of *Gymnarchus*, with its swarm of scarlet-bearded, yolk-hampered larvæ, presents a most amazing spectacle.

By the time the huge yolk-sac has been completely absorbed, the young larvæ are ready to leave the nest. They still, however, continue their ceaseless journeyings to the surface for air. It may now be noticed, however, that the passage back to the bottom of the nest is not merely a passive falling, but that the young larvæ actually

dart backwards from the surface. When the young *Gymnarchus* leaves the nest it has fully developed the characteristic cylindrical tail of the adult, and in this connection its habits are very interesting.

The *Gymnarchus* propels itself through the water, not by the action of its paired fins, not by the motion of its tail or the undulatory motion of the axis of its body, but entirely by the action of its dorsal fin. This fin extends nearly the whole length of the dorsal surface, ceasing abruptly at the commencement of the cylindrical tail. When *Gymnarchus* starts forwards, the motion is the result of a series of waves passing backwards along the dorsal fin. About five such waves are passing at a time. Suddenly the fish will proceed at the same rate in the opposite direction, and now the motion is the result of a series of waves passing forwards along the dorsal fin.

As the *Gymnarchus* swims rapidly backwards in this way, it may be seen to guide itself through the grasses by using this peculiar tail which it possesses as a feeler. Thus it appears to be quite immaterial to the fish which way it progresses, and it always appears to swim in comparatively straight lines.

How *Gymnarchus* constructs the wonderful floating nest in which it lays its eggs I have been unable to observe. The natives approach these nests with great caution, stating that the parent is at this time extremely fierce and has a very formidable bite. Both the adult fish and its eggs are greatly sought after as food.

A large number of the young fry of *Gymnarchus*, which I had caught immediately they left the nest, lived well on chopped-up worms. I tried to bring some of them to England alive, but every one died as we got into colder climes.

V.—The Nesting-habits of *Heterotis niloticus* Cuv.

In the same swamps, during the month of July, a most striking feature is the presence of numbers of enormous nests, which proved to be those of *Heterotis niloticus* (text-fig. 21). These nests measured four feet in diameter, and were made in about two feet of water. In wading through the reed-choked swamp, when one came across one of these structures they appeared like miniature lagoons. The walls of the nest were about eight inches thick at the top and compact, being made of the stems of the grasses removed by the fish from the centre of the nest. The floor of the nest was the swamp-bottom, and was made perfectly smooth and bare.

Once I watched a "Fantang," as the natives call this fish, making its nest. It was circling round and round the wall of its nest, every now and then throwing its tail upwards and outwards, tossing on to the top of the wall the débris from the inside of the nest. Thus it toiled on until the wall reached the surface of the water and was complete. When the nest was finished, the water it contained was perfectly clean and clear, so that I could see with my water-telescope the eggs nearly covering the bottom of the nest. When all the eggs are laid, the fish leaves the nest by a hole at one side.

The eggs, which measure $2\frac{1}{2}$ mm., then appear to hatch in about two days, though, owing to the distance the nests were from my quarters, of this I am not certain. The nest appears to be used for at most four or five days. As soon as the larvæ are hatched, they begin to strike up from the bottom. The day after hatching they may be seen continually passing up and down, and are now provided with long external gill-filaments of a blood-red colour, but not so numerous or so long as in the case of *Gymnarchus* (Pl. XI. fig. 6 & 7).

The following day they cease to pass up and down, and converging to a swarm about one foot in diameter, form a deep continuous circle remarkable for its regularity and

Text-fig. 21.

Nest of *Heterotis*.

persistence. The swarm occupies the exact centre of the little lagoon. The young fry, which by now have lost the long external gill-filaments, are seen to be steadily careering round and round ever in the same direction for at least a day. About the fourth day the swarm becomes less persistent and regular, the larvæ swimming first to one side of the nest and then to the other, until about the fifth day they leave the nest by the exit for a few trial trips attended by the parent, and finally leave it altogether, swimming hither and thither in a dense swarm, from which the parent is never far distant. I kept a large number of the young fry for several weeks, but could not get them to feed, and eventually they all died.

The ova of *Heterotis* are shed into the cœlom as in the Salmon. *Heterotis* belongs to the group Osteoglossidæ, which has much the same distribution as the Dipnoi, though it seems doubtful whether this points to an antiquity of the group equal to that of the Dipnoi. Günther, however, regards the Osteoglossidæ as one of the earliest types of Teleostean fishes.

VI.—The Nesting-habits of *Sarcodaces odoë* Bl.

In these same flooded grass-lands the eye is frequently caught by masses of whi t foam floating on the surface of the water. On close inspection it is seen to be filled with numerous transparent ova, about the same size as those of *Heterotis* (2½ mm.). Soon these eggs hatch, and on hatching make their way through the foam, in which they are laid, down to the surface of the water, and there the young larvæ hang holding to the surface of the water by a large adhesive organ situated on the front of the head (Pl. XI. fig. 8 & 9, *c.o.*).

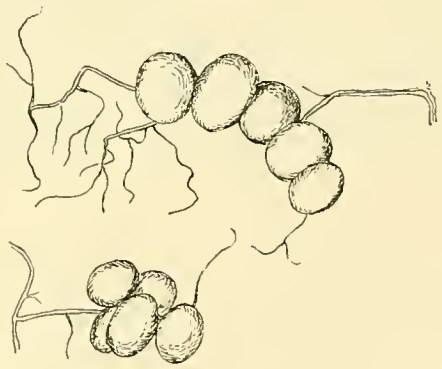
The natives assured me that these were the eggs of the Sannko, more scientifically *Sarcodaces odoë*. On rearing some of these larvæ, I was able to confirm this statement.

Sarcodaces is one of the *Characinidæ*, of which family examples occur in Africa and South America.

VII.—The Nesting-habits of *Hyperopisus bebe* Lacép.

It was a curious fact that of the six species of *Mormyridæ* which I obtained in the Gambia, only one besides *Gymnarchus* was found breeding in the swamps. This was *Hyperopisus bebe* Lacép.

Text-fig. 22.

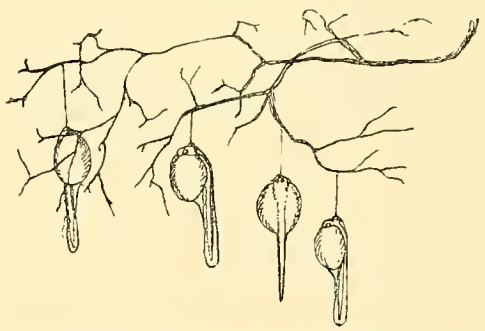


Eggs from nest, supposed to be that of *Hyperopisus bebe*.

Although I did not succeed in finding fertilized eggs of *Hyperopisus* this year, I obtained a number of females full of ripe eggs. I am practically certain that these ovarian eggs are identical with the eggs which I studied last year under the impression that they were the eggs of *Polypterus*.

These eggs were laid in shallow depressions of the swamp bottom, and attached to the rootlets of the grasses laid bare by the parent in scooping out the depression for the reception of the eggs (text-fig. 22, p. 130). The eggs are very small, about $1\frac{1}{4}$ mm. in diameter, and slightly oval, the long axis being rather over $1\frac{1}{4}$ mm. in length. They are yellowish in colour and semitransparent. The eggs hatch in four days, and are then provided with four large cement-glands situated on the top of the head, and two smaller ones on the front of the head (Pl. XI. fig. 10, *c.o.*). Immediately the larva is hatched it runs the upper part of its head against the rootlets, and wriggling away again, draws out from the four cement-glands four fine threads of viscid mucus, which are hardened by contact with the water, and form a minute rope about the length of the body of the larva. By this the larva hangs suspended for four or five days until the yolk is absorbed. If the larva is detached meanwhile, a fresh rope is formed by a fresh secretion of mucus (text-fig. 23). While hanging thus, each larva continually oscillates the whole length of its body from side to side. In one nest there are many thousands of these larvæ suspended

Text-fig. 23.



Larvæ, supposed to be those of *Hyperopisus bebe*, suspended from the rootlets in the nest.

in this way, presenting the appearance of a shaking mass of jelly, for all the larvæ oscillate themselves in unison. I was unfortunately unable to rear any of these larvæ to a stage old enough to be able to identify them.

VIII.—Conclusion.

I should here state that I had great difficulty in keeping alive any of the fish-larvæ that I found for any length of time in any but the natural conditions, *Protopterus*, however, excepted. In the case of *Gymnarchus* a great number of ways was tried, even floating perforated trays as an attempt to imitate the natural conditions. I do not so much wonder at my want of success in this as at the successful way in which the larvæ are hatched out in nature. I never found a dead larva in any

nest of *Gymnarchus*, notwithstanding that the eggs and larvæ were lying within six inches of the surface of the water, quite unprotected from the burning rays of a tropical sun and the lashing of the tropical rains. The extremes of temperature taken in the nests were 25° C. and 32°·5 C. But supposing the larvæ to be so constituted that they can withstand the changes of the weather, how is it that large conspicuous eggs in very conspicuous nests on the surface of the water escape forming the food of the abundant bird-life of these swamps?

In the breeding-habits of the last four types I have described, the interesting fact comes out that the first two and the last two each have, in common, organs in the larva which are usually regarded as not belonging to the Teleostean division of fishes. *Gymnarchus* and *Heterotis* have each, for a time, enormously elongated gill-filaments, structures which are so characteristic of Elasmobranch larvæ. Something of the kind was noticed in the development of the loach by Götte [1], but I think this is the only case of such organs in the Teleosteans. *Sarcodaces* and *Hyperopisus* have each well-developed cement-organs on the head. These structures are generally regarded as characteristic of the Ganoids. It seems, then, that the conditions by which fishes, which breed in tropical fresh waters, are surrounded is conducive to the development of very various accessory organs in the larva, both for the purpose of respiration and also of preserving them from harmful contact with their surroundings, and that these structures cannot be regarded as having any great morphological meaning. The resemblance of the embryo of *Gymnarchus* to that of an Elasmobranch I hope to discuss in a future work on the development of *Gymnarchus*.

IX.—EXPLANATION OF THE PLATES.

All the figures of Plate X. were originally drawn by myself with the aid of a camera lucida, and were then copied by Mr. Edwin Wilson.

Figs. 2, 3, 4, 5, 12, & 13 were drawn on the Gambia from living specimens. Figs. 1, 6, 7, 8, 9, 10, & 11 were drawn from formalin specimens.

The magnification is 8 diameters.

The figures in Plate XI. were all drawn by myself except fig. 1, which was from a specimen preserved in formalin, drawn by Mr. Edwin Wilson under my supervision and coloured from my notes by myself. Figs. 4, 5, 6, 7, & 8 were drawn from life on the Gambia. Fig. 3 was drawn from a specimen preserved with corrosive sublimate and acetic acid.

au., auditory sac; *bp.*, blastopore; *br.*, branchial eminences; *br.* I. II. &c., branchial arches; *c.o.*, cement-organ; *cl.*, position of cloaca; *ep.e.*, growing edge of epiblast; *Eg.* I. II. &c., external gills; *f.f.*, dorsal fin-fold; *h.l.*, hind limb; *H.*, hyoid arch; *H.br.*, hyobranchial cleft; *invag.*, line of invagination; *M.*, mandibular arch; *M.H.*, mandibulo-hyoid fold; *m.f.*, medullary folds; *o.c.*, optic outgrowth from brain; *op.*, operculum; *p.f.*, pectoral fin; *pn.*, pronephros; *s.v.g.*, groove marking rudiment of spiral valve; *sp.*, groove between mandibular and hyoid arches; *v.* IV., fourth ventricle; *y.k.*, yolk-cells.

[1] "Entwick. d. Teleostierkeime," Zool. Anz. No. 3, 1878.

PLATE X.

PLATE X.

The figures of this Plate illustrate the external features in the development of *Protopterus annectens*, Ow.

Fig. 1. Egg on the first day of observation, segmentation somewhat advanced: p. 121.

Fig. 2. Egg on the morning of the second day, showing commencement of invagination: p. 121.

Fig. 3. Egg on the evening of the second day, showing a further stage of invagination. Above is seen a transparent portion indicating the segmentation-cavity: p. 121.

Fig. 3 *a*. A variation of the stage shown in fig. 3. The area of the disappearing yolk-cells is viewed from a somewhat different aspect, in order to show that the line of invagination is not here straight but curved: p. 121.

Fig. 4. Egg on the morning of the third day, showing the straight line of invagination and the gradual disappearance of the large-celled yolk: p. 121.

Fig. 4 *a*. A variation of the stage shown in fig. 4, showing that the line of invagination is not always straight: p. 121.

Fig. 5. Egg on the evening of the third day, showing the last stage of invagination: p. 121.

Fig. 6. Egg on the morning of the fourth day, showing medullary folds encircling the blastopore: p. 122.

Fig. 7. Embryo on the evening of the fourth day, showing origin of optic outgrowths, mandibulo-hyoid fold, branchial eminence, and pronephros: p. 122.

Fig. 8. Embryo on the fifth day, showing the segmentation of the mandibulo-hyoid fold and first segmentation of branchial eminence; also the remnant of the blastopore, and the first appearance of the cement-organ, and the development of the head and tail-folds: p. 122.

Fig. 9. Embryo on the sixth day, showing the further segmentation of the branchial eminence into four: p. 122.

Fig. 10. Embryo on the seventh day, showing the first pairs of external gills strongly differentiated from the second, third, and fourth pairs. The trunk of the embryo has grown back from the main mass of yolk, taking much of the yolk with it. The true tail is not yet formed: p. 122.

Fig. 11. Larva on the eighth day, just hatched, showing further growth of the external gills, and the auditory sacs showing through the tissues. The true tail-region has now begun to grow: p. 122.

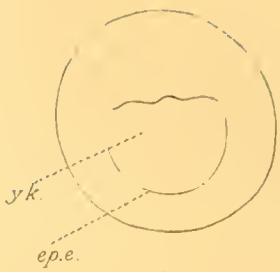
Fig. 12. Larva on the tenth day, showing the serial arrangement of the external gills, the indication of the spiracular cleft, the first trace of the hind limbs, being now anterior to the position of the cloaca, and the well-developed and functional cement-organ. The tail-fins are now well-developed. Pigment has appeared on the head: p. 123.

Fig. 13. Larva on the seventeenth day, showing general advancement, the rotation of the external gill, the operculum, the vessel in the spiral valve groove, and the well-developed limbs: p. 123.

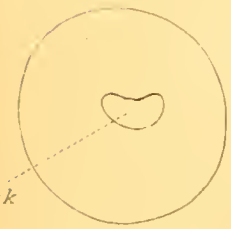
1

2

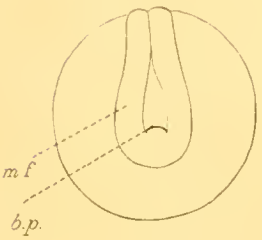
3.



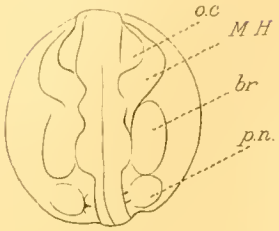
4



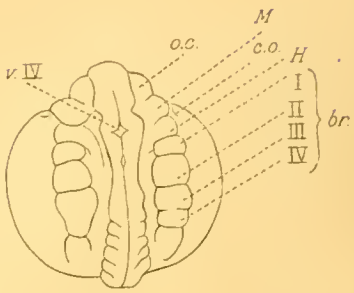
5.



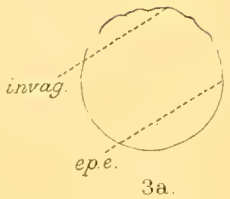
6.



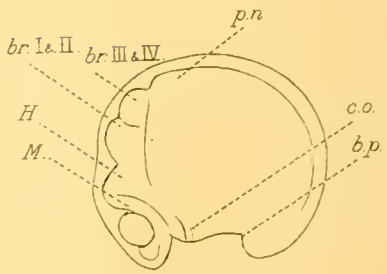
7.



9.

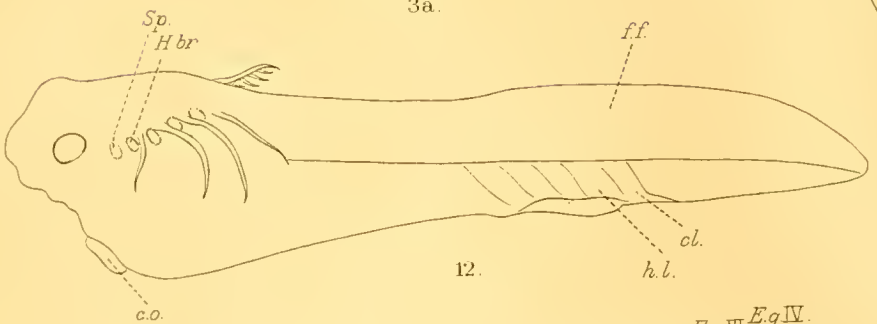


3a.

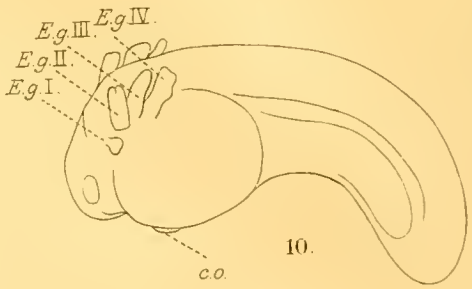


8

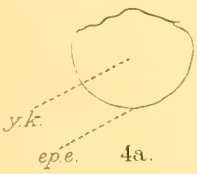
11



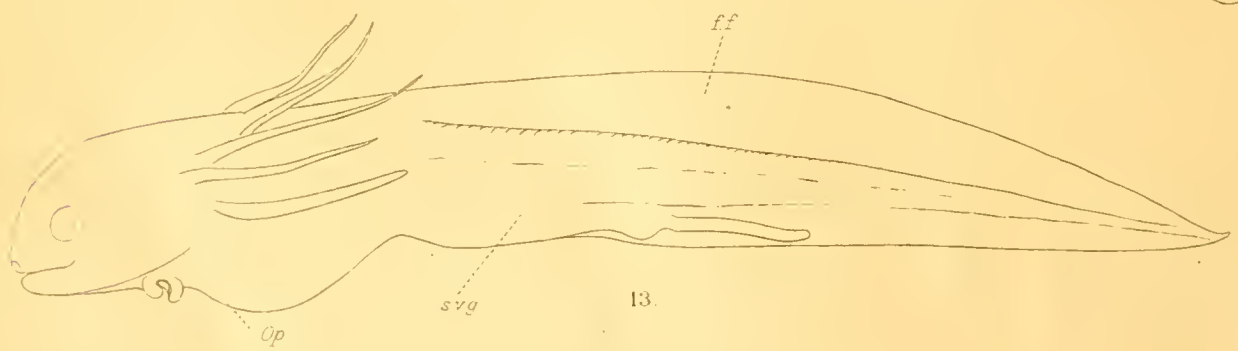
12.



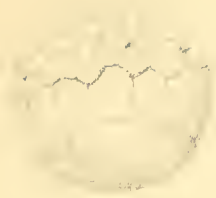
10.



4a.



13.



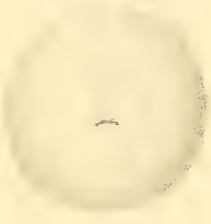
1.

2

3.

4

5.



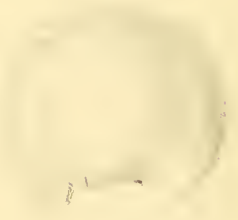
6.

7.

9.

3a.

11

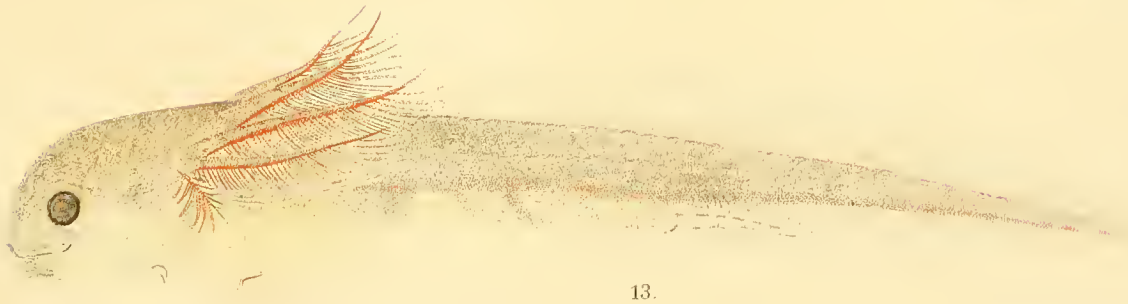


8

12.

4a.

10.



13.

J.S.B.del.

E.Wilson, Lith. Cambridge.

DEVELOPMENT OF WEST AFRICAN FISHES.

PROTOPTERUS

PLATE XI.

PLATE XI.

Fig. 1. Larva of *Polypterus lapradei* Stein., $1\frac{1}{4}$ inch in length, magnification about four diameters, showing the very large external gill of the hyoid arch, situated immediately behind the spiracle, the blood-supply to the same from the ventral aorta, and the very large size of the head and tail-region of the body, also the dorsal fin not broken up into finlets. The larva is drawn in a very characteristic attitude as observed when in the aquarium. The smallness of the alternate branches of the gill and their different position is not shown.

Fig. 2. External gill of *Polypterus lapradei*, showing the difference in size of each gill-branch : p. 118.

Fig. 3. Larva of *Protopterus annectens* Ow., a few days after leaving the nest, about one month old. The larva was killed when its chromatophores were neither fully expanded nor fully contracted. The first pair of external gills has been lost and metamorphosis is nearly complete : p. 124.

Fig. 4. Larva of *Gymnarchus niloticus* Cuv., one week after it was laid, two days after hatching, showing external gill-filaments, blood-vessel to and from yolk-sac, and the completely diphycercal tail : p. 127.

Fig. 5. Larva of *Gymnarchus*, four days later, showing long drawn-out yolk-sac and abundant external gill-filaments. The fin-folds of the tail are shown, and the first trace of differentiation of the tail to form the whip-like feeler : p. 127.

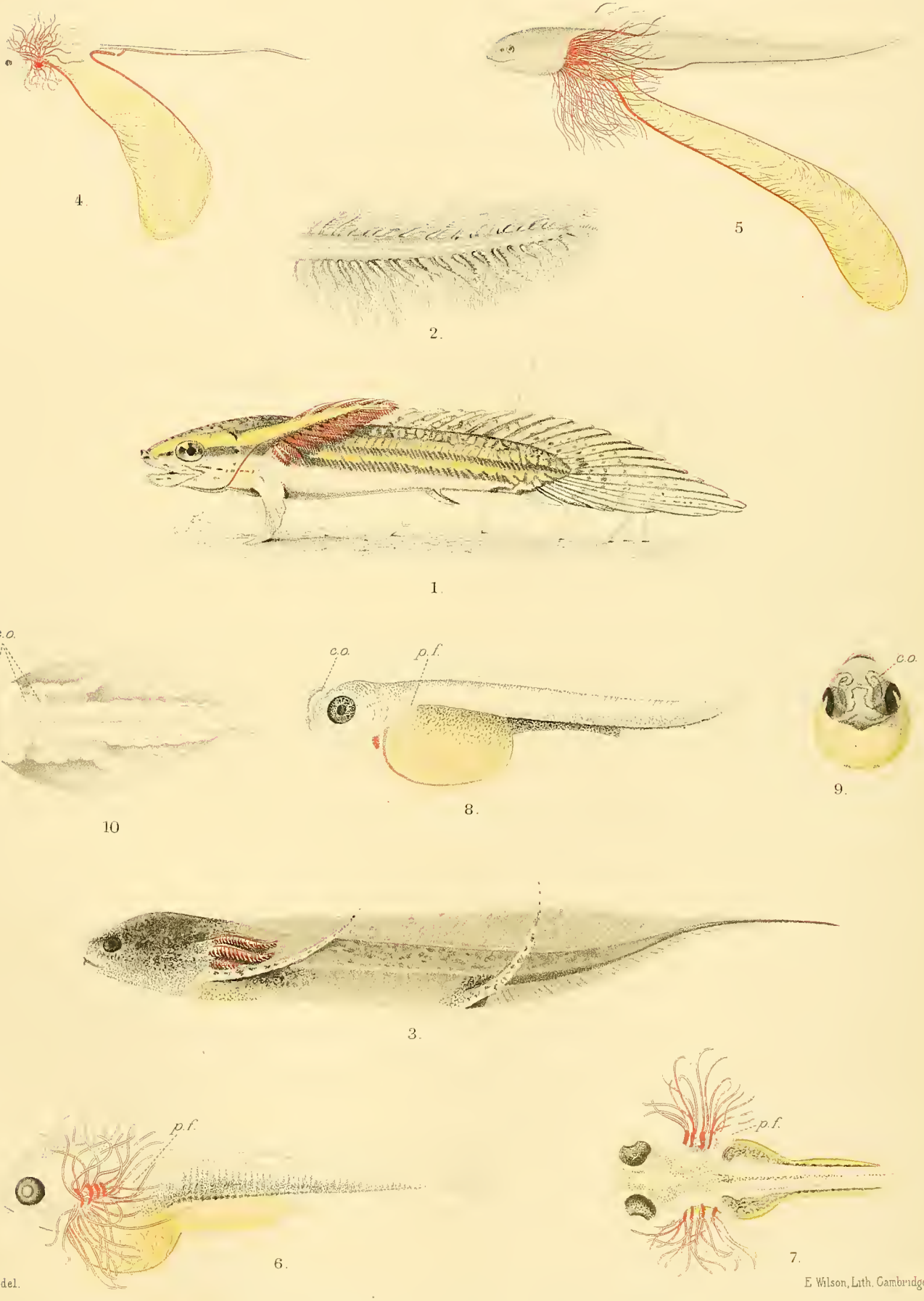
Fig. 6. Larva of *Heterotis niloticus* Cuv., one day after hatching, showing external gill-filaments, backward extension of the yolk to the cloaca, the pectoral fins, four branchial arches, developing operculum, and heterocercal rays in the tail : p. 129.

Fig. 7. Larva of *Heterotis*, dorsal aspect, in order to show relations of operculum, gills, and pectoral fin : p. 129.

Fig. 8 Larva of *Sarcodaces odoë* Bl., just after hatching, showing the large adhesive organ borne on the front of the head : p. 130.

Fig. 9. The same, frontal aspect, to show the form of the adhesive organ : p. 130.

Fig. 10. Larva of *Hyperopisus bebe* Lacép., showing the four dorsal and two frontal cement-organs, the auditory sacs, and prominent gill-folds : p. 131.



J. S. B. del.

E. Wilson, Lith. Cambridge.

DEVELOPMENT OF WEST AFRICAN FISHES.

1-2. POLYPTERUS. 3. PROTOPTERUS 4-5 GYMNARCHUS. 6-7 HETEROTIS.
8-9 SARCODACES. 10. HYPEROPISUS

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON
(continued).

		To Fellows. £	s.	d.	To the Public. £	s.	d.
VOLUME XIV. (1896–1898, containing 47 Plates) .	Price	5	5	0	7	0	0
Part 1. (1896, containing 2 Plates)	„	0	6	0	0	8	0
„ 2. (1896, containing 6 Plates)	„	0	9	0	0	12	0
„ 3. (1897, containing 9 Plates)	„	0	15	9	1	1	0
„ 4. (1897, containing 10 Plates)	„	1	10	0	2	0	0
„ 5. (1898, containing 2 Plates)	„	0	6	0	0	8	0
„ 6. (1898, containing 7 Plates)	„	0	18	0	1	4	0
„ 7. (1898, containing 6 Plates)	„	0	11	3	0	15	0
„ 8. (1898, containing 5 Plates and Title and Index)	„	0	9	0	0	12	0
VOLUME XV. (1898–1901, containing 52 Plates) .	Price	5	15	6	7	14	0
Part 1. (1898, containing 8 Plates)	„	0	15	9	1	1	0
„ 2. (1899, containing 5 Plates)	„	0	9	0	0	12	0
„ 3. (1899, containing 4 Plates)	„	0	9	0	0	12	0
„ 4. (1899, containing 4 Plates)	„	0	9	0	0	12	0
„ 5. (1900, containing 24 Plates)	„	2	12	6	3	10	0
„ 6. (1901, containing 4 Plates)	„	0	11	3	0	15	0
„ 7. (1901, containing 3 Plates and Title and Index)	„	0	9	0	0	12	0
VOLUME XVI.							
Part 1. (1901, containing 6 Plates)	Price	0	18	0	1	4	0
„ 2. (1901, containing 5 Plates)	„	0	11	3	0	15	0

CONTENTS.

II. *Contribution towards a Knowledge of the Osteology of the Pigmy Whale* (Neobalæna marginata). *By* Frank E. Beddard, *M.A., F.R.S., Prosector and Vice-Secretary of the Society.* (Plates VII.–IX.) . . . . . page 87

III. *On the Breeding-habits of some West-African Fishes, with an Account of the External Features in Development of* Protopterus annectens, *and a Description of the Larva of* Polypterus lapradei. *By* J. S. Budgett, *M.A., F.Z.S., Trinity College, Cambridge.* (Plates X. & XI.) 115

THE PUBLICATIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

The scientific publications of the Zoological Society of London are of two kinds—"Proceedings," published in an octavo form, and "Transactions," in quarto.

According to the present arrangements, the "Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the "Proceedings" by the Committee of Publication. A large number of coloured plates and engravings are attached to each annual volume of the "Proceedings," to illustrate the new or otherwise remarkable species of animals described in them. Among such illustrations, figures of the new or rare species acquired in a living state for the Society's Garden are often given.

The "Proceedings" for each year are issued in four parts, on the first of the months of June, August, October, and April, the part published in April completing the volume for the last half of the preceding year. Commencing from January 1901 they form two half-yearly volumes.

The "Transactions" contain such of the more important communications made to the scientific meetings of the Society as, on account of the nature of the plates required to illustrate them, are better adapted for publication in the quarto form. They are issued at irregular intervals.

Fellows and Corresponding Members, upon payment of a Subscription of £1 1*s.* before the day of the Anniversary Meeting in each year, are entitled to receive all the Society's Publications for the year. They are likewise entitled to purchase the Publications of the Society at 25 per cent. less than the price charged for them to the Public. A further reduction of 25 per cent. is made upon purchases of Publications issued prior to 1871, if they exceed the value of five pounds.

Fellows also have the privilege of subscribing to the Annual Volume of the 'Zoological Record' for a sum of £1 (which includes delivery in the United Kingdom *only*), but this privilege only holds good if the subscription is paid before the First of December in each year.

Such of these publications as are in stock may be obtained at the Society's Office (3 Hanover Square, W.), at Messrs. Longmans', the Society's publishers (Paternoster Row, E.C.), or through any bookseller.

August, 1901.

P. L. SCLATER,
Secretary.

TRANSACTIONS

OF

THE ZOOLOGICAL SOCIETY

OF LONDON.

VOL. XVI.—PART 3.

LONDON:

PRINTED FOR THE SOCIETY,

SOLD AT THEIR HOUSE IN HANOVER-SQUARE;

AND BY MESSRS. LONGMANS, GREEN, AND CO., PATERNOSTER-ROW

October 1901.

Price 21*s*.

Taylor and Francis, Printers,] [Red Lion Court, Fleet Street.

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

	To Fellows. £ s. d.	To the Public. £ s. d.
VOLUME I. (1833–1835, containing 59 Plates) . . Price	3 13 6	4 18 0*
VOLUME II. (1835–1841, containing 71 Plates) . . „	4 0 0	5 6 6*
VOLUME III. (1842–1849, containing 63 Plates) . . „	3 8 3	4 11 0*
VOLUME IV. (1851–1862, containing 77 Plates) . . „	6 2 0	8 2 6†
VOLUME V. (1862–1866, containing 67 Plates) . . „	5 4 3	6 19 0†
VOLUME VI. (1866–1869, containing 92 Plates) . . „	11 5 0	15 0 0†
VOLUME VII. (1869–1872, containing 73 Plates) . . „	10 4 0	13 12 0†
VOLUME VIII. (1872–1874, containing 82 Plates) . „	9 8 3	12 11 0†
VOLUME IX. (1875–1877, containing 99 Plates) . . „	12 1 6	16 2 0†
VOLUME X. (1877–1879, containing 95 Plates) . . „	10 0 3	13 7 0†
GENERAL INDEX, Vols I. to X. (1833–1879) . „	0 7 6	0 10 0
VOLUME XI. (1880–1885, containing 97 Plates) . . „	9 12 0	12 16 0
VOLUME XII. (1886–1890, containing 65 Plates) . . „	5 8 0	7 4 0
VOLUME XIII. (1891–1895, containing 62 Plates) . . „	6 8 3	8 11 0

* No copies of these volumes remain in stock.

† Only complete copies of these volumes are left in stock.

Continued on page 3 of Wrapper.

IV. *Third Contribution to the Ichthyology of Lake Tanganyika.—Report on the Collection of Fishes made by Mr. J. E. S. Moore in Lakes Tanganyika and Kivu during his Second Expedition*, 1899–1900. *By* G. A. Boulenger, *F.R.S.*, *F.Z.S.*

Received and read January 15, 1901.

[Plates XII.–XX.]

In presenting this report on the second collection made in Lake Tanganyika by Mr. Moore [1], I may at once state that the expectations held out in the first report, as to the possible occurrence, in the greater depths of the lake, of forms differing fundamentally from the typically African freshwater forms, have not been in any way realized. Although fully equipped for a complete survey of the lake, both on its shores and in its depths, which we know to extend beyond 300 fathoms, the Tanganyika Expedition organized by Professor Ray Lankester has failed to bring home representatives of any but the few families already known from the lake, and which occur also in the other basins of Tropical Africa [2]. Its results only further emphasize the striking fact of the extraordinary multitude and diversity of the Cichlid

[1] For an account of the Expedition, *cf.* Geographical Journal, vol. xvii. 1901, p. 1.

[2] Since the publication of the first report, in which lists were given of the fishes of the principal lakes of Central Africa, the ichthyological fauna of Lake Mwern, which, from its vicinity to Tanganyika, is of special interest, has become known through collections made by Mr. Alfred Sharpe, C.B., and the Lemaire Expedition (Congo Free State). It enables me to draw up the following list, in which the names of the endemic species are printed in italic, the general habitat of the others being given in brackets :—

Mormyridæ.

1. Gnathonemus stanleyanus Blgr. (Congo).
2. Mormyrus longirostris Peters (Nile, Congo, Zambesi).

Characinidæ.

3. Hydrocyon lineatus Blkr. (Senegal to Congo, Tanganyika, Zambesi).
4. Alestes macrophthalmus Gthr. (Gaboon, Ogowe, Congo, Tanganyika).
5. Alestes *lemairii* Blgr.

Siluridæ.

6. Schilbe mystus L. (?) (Nile, Calabar, Congo).
7. Chrysichthys *sharpii* Blgr.
8. Anchenoglanis biscutatus Geoffr. (Nile, Trop. Africa).
9. Synodontis zambesensis Ptrs. (Zanzibar to Mozambique, Nyasa).
10. Synodontis ornatipinnis Blgr. (Congo).

Cichlidæ.

11. Paratilapia *macrocephala* Blgr.
12. Paratilapia *mocruensis* Blgr.
13. Tilapia natalensis M. Web. (Congo, E. & S.E. Africa).
14. Tilapia *polyacanthus* Blgr.

Perciform Fishes, a very natural group the habitat of which extends over the fresh waters of the whole of Africa, Madagascar, South-western Asia, Southern India and Ceylon, and Central and South America. They also confirm the no less remarkable negative feature of the absence of Mormyrids, a family so eminently characteristic of the Ethiopian fresh waters, occurring as they do in all the rivers of Tropical Africa, and in all the lakes north and south of Tanganyika. Lastly, they add to the list of Cyprinids, and bring out the interesting fact of the presence in that lake of a species of *Capoëta*, which genus, well represented in Southern Asia, was known in Africa from a single species inhabiting Abyssinia. But the general conclusions which could be drawn from the study of the first collection require no modification.

An important addition has been made to our knowledge of the Central-African lakes through Mr. Moore's investigation of Lake Kivu, to the north of Tanganyika, and overflowing into the latter through the Rusisi River, but without any communication with any other basin, and this investigation has failed to throw any light on the problem of the halolimnic fauna. With regard to the piscine inhabitants of Kivu, the information gained goes simply to show that its waters are very thinly populated. Its former connection with the Nile, at probably no very remote period, geologically speaking, as ascertained by the Expedition, may account for the presence of *Tilapia nilotica*, a species which has not been found in the Tanganyika nor in the Congo Basin. Along with it were obtained examples of another *Tilapia* (*T. burtoni*) previously known from Tanganyika, a *Paratilapia* (*P. bloyeti*) described from East Africa, a new species of the same genus, and a new *Barbus*. No representatives could be found of any of the numerous generic types of *Cichlidæ* which are the essential feature of the fish-fauna of the great lake.

The number of specimens brought home on this occasion from Tanganyika and Kivu amounts to 190, representing 50 species, 26 of which were new to science, obtained at the following localities, enumerated from south to north, as well as from far out in Lake Tanganyika:—

Kinyamkolo, extreme south end of Lake Tanganyika.
Kalambo, S.E. of lake.
Tembwi, W. coast, 35 or 40 miles S. of Albertville.
Msambu, E. coast, S. of middle.
Kibogo, E. coast, middle of lake.
Kibwesi, near Kibogo.
Maswa, E. coast, about 50 miles S. of Ujiji.
Usambura, N. end of lake.
Rusisi R., at mouth.
Rusisi R., at source.
L. Kivu.

In the introduction to the first Report, I tabulated the species then known from

Lake Tanganyika and made up a list of 43 species. Through the collections formed since by the Officers of the Congo Free State and by Mr. Moore, the number has now risen to 91—that is, nearly as many as are known from the Nile (anadromous and catadromous species not included). Out of these 91 species it has been my privilege to describe as many as 74, and I beg on this occasion to express my most grateful thanks to my friend Mr. Moore, and to my fellow-countrymen in the service of the Congo Free State, for having placed in my hands the valuable material brought home at the cost of so great perils and hardships.

List of the Fishes of Lakes Tanganyika and Kivu.

The names of the genera and species peculiar to these lakes are printed in italic, the others in roman, in the Table (pp. 140–141).

The 7 columns refer to the various collections on which the list is based :—

1. Mr. Coode Hore's Collection (Günther, P. Z. S. 1893, p. 628).
2. Mr. Moore's first Collection (Boulenger, Tr. Zool. Soc. xv. 1898, p. 1).
3. Capt. Descamps's Collection (Boulenger, *l. c.*).
4. Lieut. Lemaire's Collection (Boulenger, *op. cit.* 1899, p. 87).
5. Capt. Hecq's Collection (Boulenger, Ann. Mus. Congo, Zool. i. 1899 & 1900).
6. Mr. Moore's second Collection from Tanganyika.
7. Mr. Moore's Collection from Kivu.

In the eighth column the range outside the Tanganyika district is indicated.

The following deductions may be drawn from the Table:—

1. Endemic genera occur only in the family *Cichlidæ*, but these are remarkably numerous (17), nearly equalling in number those known from all other parts of the world.
2. Most of the species of *Cichlidæ* and all the *Cyprinidæ* and *Mastacembelidæ* are endemic, whilst all the *Characinidæ* and one-half the *Siluridæ* have a much wider range.
3. Not one of the collections yet made contains representatives of much more than one-half of the known species [1], and out of the six species represented in the first collection (Mr. Coode Hore's) only three have been rediscovered.

[1] Mr. Moore wishes me to observe, however, that, owing to the difficulties of transport, he abstained in many cases from preserving specimens of the species which he felt certain of having obtained on his first expedition. The fact nevertheless remains that the collections made by him are so far from being duplicated by those received from the Belgian explorers as to show our knowledge of the Fishes of the lake to be still far from complete. Although Mr. Moore fished not far from Albertville, it is surprising how many species discovered about the latter place by Capt. Hecq are unrepresented in his collection. He also fished near Ujiji, and yet examples of only two out of the six species described by Dr. Günther from Mr. Coode Hore's collection have turned up again.

	1.	2.	3.	4.	5.	6.	7.	
POLYPTERIDÆ.								
1. Polypterus congicus Blgr. 1898	..	..	..	..	..	*	..	Congo.
LEPIDOSIRENIDÆ.								
2. ? Protopterus æthiopicus Heck. 1851	..	..	..	..	..	..	..	Upp. Nile, E. Africa.
CHARACINIDÆ.								
3. Hydrocyon lineatus Blkr. 1863	..	*	..	*	*	*	..	[E. Africa. Senegal to Congo,
4. Alestes macrophthalmus Gthr. 1867	..	*	..	*	*	*	..	Congo, Gaboon,
5. „ macrolepidotus C. & V. 1849	..	*	..	*	..	*	..	Nile. [Ogowe.
6. Citharinus gibbosus Blgr. 1899	..	..	..	..	..	*	..	Congo.
CYPRINIDÆ.								
7. Capoëta *tanganicæ* Blgr. 1900	..	..	..	..	..	*		
8. Barbus *platyrhinus* Blgr. 1900	..	..	..	..	..	*		
9. „ *altianalis* Blgr. 1900	..	..	..	..	..	..	*	
10. „ *serrifer* Blgr. 1900	..	..	..	..	..	*		
11. „ *tropidolepis* Blgr. 1900	..	..	..	..	*	*		
12. Barilius *moorii* Blgr. 1900	..	..	..	..	..	*		
13. „ *tanganicæ* Blgr. 1900	..	..	..	..	..	*		
SILURIDÆ.								
14. Clarias robecchii Vincig. 1893	..	*	..	..	..	..	..	Somaliland,
15. „ *liocephalus* Blgr. 1898	..	*						[Zanzibar.
16. Chrysichthys cranchii Leach, 1810	..	..	..	*	*	..	..	Congo.
17. „ *myriodon* Blgr. 1900	..	..	..	..	*	*		
18. „ *brachynema* Blgr. 1900	..	..	..	..	..	*		
19. Auchenoglanis biscutatus Geoffr. 1829	..	*	..	*	*	*	..	Nile, Trop. Africa.
20. Anoplopterus platychir Gthr. 1864	..	*	..	..	..	..	..	E. Africa, Nyassa.
21. Synodontis *granulosus* Blgr. 1900	..	..	..	..	..	*		
22. „ *multipunctatus* Blgr. 1898	..	*	..	*	*	*		
23. Malopterurus electricus Lacép. 1801	..	*	..	*	*	*	..	Nile, Trop. Africa.
CYPRINODONTIDÆ.								
24. Haplochilus *tanganicanus* Blgr. 1898	..	*	..	*				
SERRANIDÆ.								
25. Lates *microlepis* Blgr. 1898	..	*	..	*	*	*		
CICHLIDÆ.								
26. Lamprologus *tetracanthus* Blgr. 1899	..	..	..	..	*			
27. „ *elongatus* Blgr. 1898	..	*	..	..	*			
28. „ *tretocephalus* Blgr. 1899	..	..	..	..	*			
29. „ *modestus* Blgr. 1898	..	*	..	..	*			
30. „ *lemairii* Blgr. 1899	..	..	..	*	..	*		
31. „ *hecqui* Blgr. 1899	..	..	..	..	*			
32. „ *moorii* Blgr. 1898	..	*						
33. „ *brevis* Blgr. 1899	..	..	..	..	*			
34. „ *compressiceps* Blgr. 1898	..	*						
35. „ *fasciatus* Blgr. 1898	..	*						
36. „ *furcifer* Blgr. 1898	..	*	..	..	..	*		

	1.	2.	3.	4.	5.	6.	7.	
37. *Julidochromis ornatus* Blgr. 1898	..	*						
38. Paratilapia *vittata* Blgr. 1901	..	..	..	..	..	..	*	
39. ,, *aurita* Blgr. 1901	..	..	..	..	..	*		
40. ,, bloyeti Sauv. 1883	.	..	..	..	..	..	*	E. Africa.
41. ,, *pfefferi* Blgr. 1898	..	*						
42. ,, *calliura* Blgr. 1901	..	..	..	..	..	*		
43. ,, *macrops* Blgr. 1898	..	*	..	..	*			
44. ,, *ventralis* Blgr. 1898	..	*						
45. ,, *dewindti* Blgr. 1899	..	..	..	*				
46. ,, *furcifer* Blgr. 1898	..	*						
47. ,, *stenosoma* Blgr. 1901	..	..	..	..	..	*		
48. ,, *leptosoma* Blgr. 1898	..	*	..	..	..	*		
49. ,, *nigripinnis* Blgr. 1901	..	..	..	..	..	*		
50. *Bathybates ferox* Blgr. 1898	..	*	..	*	*	*		
51. ,, *fasciatus* Blgr. 1901	..	..	..	..	..	*		
52. Pelmatochromis *polylepis* Blgr. 1901	..	..	..	..	*	*		
53. *Ectodus descampsii* Blgr. 1898	..	..	*	*				
54. ,, *melanogenys* Blgr. 1898	..	..	*	*				
55. ,, *longianalis* Blgr. 1899	..	..	..	*	..	*		
56. *Xenotilapia sima* Blgr. 1899	..	..	..	*	*			
57. ,, *ornatipinnis* Blgr. 1901	..	..	..	..	..	*		
58. *Grammatotria lemairii* Blgr. 1899	..	..	..	*	*			
59. *Trematocara marginatum* Blgr. 1899	..	..	..	*	*	*		
60. ,, *unimaculatum* Blgr. 1901	..	..	..	..	..	*		
61. *Telmatochromis vittatus* Blgr. 1898	..	*						
62. ,, *temporalis* Blgr. 1898	..	*	..	..	*	*		
63. *Gephyrochromis moorii* Blgr. 1901	..	..	..	..	..	*		
64. *Tropheus moorii* Blgr. 1898	..	*						
65. ,, *annectens* Blgr. 1900	..	..	..	..	*			
66. *Simochromis diagramma* Gthr. 1893	*	*	..	..	..	*		
67. Tilapia nilotica L. 1757	..	..	..	..	..	..	*	Syria, Nile, Sene-
68. ,, *burtoni* Gthr. 1893	*	..	..	..	*	..	*	[gambia, Niger.
69. ,, *horii* Gthr. 1893	*							
70. ,, *rubropunctata* Blgr. 1899	..	..	..	*	*			
71. ,, *dardennii* Blgr. 1899	..	..	..	*	*	*		
72. ,, *labiata* Blgr. 1898	..	*	..	*	*	*		
73. ,, *pleurotænia* Blgr. 1901	..	..	..	..	..	*		
74. ,, *trematocephala* Blgr. 1901	..	..	..	..	..	*		
75. ,, *boops* Blgr. 1901	..	..	..	..	..	*		
76. ,, *grandoculis* Blgr. 1899	..	..	..	*				
77. ,, *microlepis* Blgr. 1899	..	..	..	*	*	*		
78. *Petrochromis polyodon* Blgr. 1898	..	*						
79. ,, *tanganicæ* Gthr. 1893	*	..	..	..	*	*		
80. *Asprotilapia leptura* Blgr. 1901	..	..	..	..	..	*		
81. *Eretmodus cyanostictus* Blgr. 1898	..	*	..	..	*			
82. *Spathodus erythrodon* Blgr. 1900	..	..	..	..	*			
83. *Perissodus microlepis* Blgr. 1898	..	*						
84. *Xenochromis hecqui* Blgr. 1899	..	..	..	..	*	*		
85. *Plecodus paradoxus* Blgr. 1898	..	..	*	..	*			
MASTACEMBELIDÆ.								
86. Mastacembelus *frenatus* Blgr. 1901	..	..	..	..	..	*		
87. ,, *moorii* Blgr. 1898	..	*						
88. ,, *ellipsifer* Blgr. 1899	..	..	..	..	*			
89. ,, *tanganicæ* Gthr. 1893	*							
90. ,, *tæniatus* Blgr. 1901	..	..	..	..	..	*		
91. ,, *ophidium* Gthr. 1893	*							

I am therefore disposed to conclude that we do not know much more than one-half of the species which will ultimately be found to inhabit Lake Tanganyika.

As regards facts of distribution, I can only emphasize again the quite extraordinary abundance and variety of the *Cichlidæ*, the salient feature of the Lake which might be named the kingdom of the *Cichlidæ*: 60 species (divided into 21 genera), being more than are known from the whole of the rest of Africa (including Madagascar) with Syria, and about as many as can be listed from South America.

As to the affinity shown by the Tanganyika Fish-fauna to other basins of Africa, we may at once dismiss all connection with Nyasa and the Zambesi. Of the genera that are not ubiquitous in Tropical Africa, two (*Capoëta* and *Anoplopterus*) have representatives in East Africa only, and two (*Lamprologus* and *Pelmatochromis*) in the Congo and West Africa only; whilst of the species, five occur also in the Nile or East Africa, and four in the Congo. We are therefore justified in concluding that this fauna shows no more special affinity to the one watershed than to the other.

List of the Fishes represented in the Collection, with Descriptions of the new Genera and Species [1].

CROSSOPTERYGII.

Polypteridæ.

1. Polypterus congicus Blgr.

Four specimens were brought home of the large *Polypterus* observed by Mr. Moore on his first visit, and identified by him under the provisional name of *P. bichir*. They prove to be referable to the allied species from the Congo, described by me in 1898 as *P. congicus* (Ann. & Mag. N. H. [7] ii. p. 418).

Particulars are appended of the four specimens, from the middle of the lake off Kalambo, at about 5 fathoms, caught in trammel-nets:—

	1.	2.	3.	4.
Total length (in millimetres)	620	580	530	520
Length of head (in millimetres)	130	110	105	100
Number of dorsal spines	13	13	14	13
Number of scales along the side	56	55	57	57
Number of scales round the body	47	47	47	47
Number of scales between occiput and first dorsal spine.	14	14	12	13

A small azygous shield usually separates the nasals in this species; it is, however, absent in two of the specimens (3, 4).

[1] Of which preliminary diagnoses have already appeared in Ann. & Mag. N. H. (7) vi. 1900, p. 478, and vii. 1900, p. 1.

The dark transverse bands, 6 to 8 in number, characteristic of this species, are very strongly marked in one of the specimens.

The ascertained range of this *Polypterus* in the Congo is from the region of the cataracts to the Stanley Falls.

TELEOSTEI.

Characinidæ.

2. Alestes macrophthalmus Gthr.

When this species was first recorded from Lake Tanganyika, it was only known from the Gaboon. It has since been found in Lake Mweru and in the Congo.

3. Alestes macrolepidotus C. & V.

Kalambo.

4. Citharinus gibbosus Blgr.

Kalambo. The largest specimen measures 500 millim.

When I described this fine fish from the Congo, I expressed the opinion that it would probably turn out to be the same as one of which I had seen a coloured sketch made by Mr. Moore on his first expedition.

Cyprinidæ.

5. Capoëta tanganicæ. (Plate XII. fig. 1.)

Boulenger, Ann. & Mag. N. H. (7) vi. 1900, p. 478.

Depth of body $3\frac{3}{4}$ to 4 times in total length, length of head 5 times. Snout broad and rounded, as long as or slightly longer than the eye, the diameter of which is $3\frac{1}{2}$ times in the length of the head and nearly twice in the interocular width; the width of the mouth equals $\frac{2}{3}$ that of the head; a minute barbel, hidden under the lip at the angle of the mouth. Dorsal III 9; third ray very strong, ossified, smooth; the fin, which is equally distant from the eye and from the caudal, has the free edge notched, and its greatest depth equals the length of the head. Anal III 5; the longest ray measures $\frac{3}{4}$ the length of the head. Pectoral acutely pointed, as long as the head, not reaching the ventral, which is inserted under the first rays of the dorsal. Caudal forked. Caudal peduncle twice as long as deep. Scales 68–70 $\frac{13-14}{14-15}$, 9 or 10 between the lateral line and the root of the ventral. Olive above, each scale darker at the base, silvery white beneath; fins greyish.

Total length 320 millim.

Three specimens from the north end of Lake Tanganyika.

The discovery of a species of this genus in Lake Tanganyika is particularly interesting from the fact that only one was known from Africa, viz. the Abyssinian

C. dilloni C. & V.; this is distinguished by the absence of barbels and the greater size of the scales (30 to 32 in the lateral line). In the presence of a pair of barbels and the small size of the scales, *C. tanganicæ* belongs to the typical section of the genus, inhabiting South-western Asia; but it has the enlarged dorsal ray neither feeble as in *C. fundulus* Pall. and allied species, nor serrated as in *C. trutta* Heck.

6. Barbus platyrhinus. (Plate XII. fig. 2.)

Boulenger, Ann. & Mag. N. H. (7) vi. 1900, p. 479.

Depth of body $3\frac{1}{4}$ times in total length, length of head 4 times. Snout broad and rounded, twice as long as the diameter of the eye, which is contained $5\frac{1}{2}$ times in the length of the head and $2\frac{1}{2}$ times in the interocular width; mouth small, with two pairs of subequal barbels, the length of which equals the diameter of the eye. Dorsal III 8; third ray not enlarged, not serrated; the fin, which is equally distant from the eye and from the caudal, has the free edge convex. Anal III 5, the longest ray not quite $\frac{2}{3}$ the length of the head. Pectoral a little shorter than the head, not reaching the ventral, which is inserted below the middle of the dorsal. Caudal forked. Caudal peduncle $1\frac{2}{3}$ as long as deep. Scales 40 $\frac{5\frac{1}{2}-6\frac{1}{2}}{5\frac{1}{2}}$, $3\frac{1}{2}$ between the lateral line and the root of the ventral. Olive-brown above the lateral line, golden yellow beneath.

Total length 390 millim.

A single specimen from south of Usambura.

This species appears to be more nearly related to *B. capensis*, Smith, from which it differs in the much shorter and broader snout.

7. Barbus altianalis. (Plate XIII. fig. 1.)

Boulenger, Ann. & Mag. N. H. (7) vi. 1900, p. 479.

Depth of body equal to or slightly greater than the length of the head, which is contained 4 to $4\frac{1}{2}$ times in the total length. Snout moderately broad, rounded, scarcely projecting beyond the lower jaw, $1\frac{1}{2}$ to $1\frac{2}{3}$ times as long as the diameter of the eye, which is contained 5 to $5\frac{1}{2}$ times in the length of the head and twice to twice and one-fourth in the interocular width; mouth small, with two pairs of subequal barbels, the length of which equals or exceeds a little the diameter of the eye. Dorsal III–IV 9; third or fourth ray very strong, ossified, not serrated; the fin, which is equally distant from the occiput and from the caudal, has the free edge notched and its greatest depth is but slightly less than the length of the head. Anal III 5; the longest ray measures about $\frac{5}{6}$ the length of the head; the fin, when folded, reaches nearly the root of the caudal. Pectoral a little shorter than the head, not reaching the ventral, the first ray of which corresponds to the origin of the dorsal. Caudal forked. Caudal peduncle nearly twice as long as deep. Scales 34–35 $\frac{6\frac{1}{2}}{5\frac{1}{2}}$, 3 between the lateral line and the root of the ventral. Olive-brown, very dark above.

Total length 450 millim.

Two specimens from Lake Kivu and one from the source of the Rusisi River.

B. altianalis is extremely closely related to *B. mariquensis* Smith. It differs only in the somewhat broader snout, the stronger third dorsal ray, and the somewhat longer caudal peduncle.

8. Barbus serrifer. (Plate XIV. fig. 1.)

Bouleng. Ann. & Mag. N. H. (7) vi. 1900, p. 479.

Depth of body 3 to $3\frac{1}{2}$ times in total length, length of head 4 to $4\frac{1}{3}$ times. Snout rounded, not projecting beyond the lower jaw, as long as or a little longer than the diameter of the eye, which is contained 4 to $4\frac{1}{3}$ times in the length of the head and $1\frac{1}{3}$ to $1\frac{1}{2}$ times in the interocular width; mouth small, with two pairs of barbels, the posterior of which are the longer and measure twice the diameter of the eye. Dorsal III 7; third ray very strong, ossified, serrated behind; the fin, which is equally distant from the eye and from the caudal, is not notched and the largest ray is a little shorter than the head. Anal III 5, the longest ray $\frac{3}{5}$ the length of the head. Pectoral $\frac{3}{4}$ to $\frac{4}{5}$ the length of the head, reaching, or nearly reaching, the base of the ventral, the last ray of which falls under the first of the dorsal. Caudal forked. Caudal peduncle $1\frac{1}{2}$ to $1\frac{2}{3}$ as long as deep. Scales 28–30 $\frac{4\frac{1}{2}-5\frac{1}{2}}{5\frac{1}{2}}$, 3 between the lateral line and the root of the ventral. Olive-brown above, silvery white beneath; a greyish stripe along each side of the body above the lateral line; a small blackish spot at the base of the caudal.

Total length 120 millim.

Three specimens from the north end of Lake Tanganyika.

Allied to *B. kessleri* Stdr. Distinguished by the smaller eye, the longer barbels, the more numerous scales, and the presence of only 7 branched dorsal rays.

9. Barbus tropidolepis. (Plate XIII. fig. 2.)

Bouleng. Ann. Mus. Congo, Zool. i. p. 133, pl. xlix. fig. 2 (1900).

Depth of body 3 times in total length, length of head 4 to $4\frac{1}{2}$ times. Snout broad and rounded, strongly projecting beyond the mouth, $1\frac{1}{2}$ to twice as long as the diameter of the eye, which is contained $4\frac{1}{2}$ to $5\frac{1}{2}$ times in the length of the head and 2 to $2\frac{1}{2}$ times in the interocular width; mouth small, inferior; a minute barbel almost entirely concealed in the angle of the lips. Dorsal III 9; third ray very strong, ossified, not serrated, its length at least $\frac{2}{3}$ that of the head; the fin, which is equally distant from the occiput and the root of the caudal, is notched. Anal II 5, the longest ray about $\frac{3}{4}$ the length of the head. Pectoral about $\frac{3}{4}$ the length of the head, not reaching the base of the ventral, the first ray of which falls under the origin of the dorsal. Caudal forked. Caudal peduncle $1\frac{1}{2}$ to $1\frac{3}{4}$ as long as deep. Scales 44–46 $\frac{8\frac{1}{2}}{8\frac{1}{2}}$, 5 between the lateral line and the root of the ventral; in breeding specimens, the scales, those at least which are above the lateral line on the caudal portion of the body, bear a median

swelling or obtuse keel, these keels forming together very regular longitudinal lines. Olive above, silvery white beneath.

This handsome fish, which grows to a length of three feet, and the flesh of which is much esteemed, was discovered almost simultaneously at Albertville by Capt. Hecq and at Usambura by Mr. Moore.

10. Barilius moorii. (Plate XIV. figs. 2, 2 *a*.)

Boulenger. Ann. & Mag. N. H. (7) vi. 1900, p. 480.

Depth of body equal to length of head, 4 times in total length. Head a little over twice as long as broad, with slightly curved upper profile; snout pointed, not extending beyond the lower jaw, as long as or a little longer than the diameter of the eye, which is contained 4 to $4\frac{1}{2}$ times in the length of the head; interorbital width a little greater than the diameter of the eye; mouth extending to below the anterior third or the centre of the eye; no barbels; the naked space between the præopercle and the suborbitals less than half the width of the latter. Gill-rakers very short, almost rudimentary, 8 on lower part of anterior arch. Dorsal III 9, originating at equal distance from the anterior border of the eye and the root of the caudal; its border is not notched, and its depth equals about $\frac{2}{3}$ the length of the head. Anal III 13-14, originating under the middle of the dorsal; its anterior rays a little longer than those of the dorsal and much longer than the posterior rays, forming a rounded lobe. Pectoral pointed, shorter than the head, not reaching the ventral, which extends to the origin of the anal. Caudal forked. Caudal peduncle twice as long as deep. Scales 56–60 $\frac{10\text{-}11}{7}$, 3 between the lateral line and the root of the ventral. Silvery, brownish on the back; more or less distinct dark vertical bars on the side of the body, about 10 in number; dorsal blackish at the end.

Total length 115 millim.

Several specimens from the north end of Lake Tanganyika.

11. Barilius tanganicæ. (Plate XIV. figs. 3, 3 *a*.)

Boulenger. Ann. & Mag. N. H. (7) vi. 1900, p. 480.

Depth of body equal to length of head, $4\frac{1}{4}$ times in total length. Head a little over twice as long as broad, with straight declivous upper profile; snout very pointed, not extending below the lower jaw, once and a half the diameter of the eye, which is contained $5\frac{1}{3}$ times in the length of the head; interorbital width once and a half the diameter of the eye; mouth extending to below the posterior border of the eye; no barbels; the naked space between the præopercle and the suborbitals about $\frac{1}{3}$ the width of the latter. Gill-rakers short, 10 on lower part of anterior arch. Dorsal III 10, originating at equal distance from the occiput and the root of the caudal, the posterior third of its base above the anal; its anterior rays are longest, measuring a little more than half the length of the head. Anal III 17, strongly notched, with rounded

anterior lobe, the longest rays of which measure $\frac{2}{3}$ the length of the head, whilst the posterior rays measure barely $\frac{1}{4}$. Pectoral pointed, $\frac{3}{4}$ length of head, not reaching the ventral, which extends to the vent. Caudal forked. Caudal peduncle a little over twice as long as deep. Scales 82 $\frac{13}{7}$, 4 between the lateral line and the root of the ventral. Silvery, olive on the back; 16 or 17 blackish vertical bars on each side of the body, equally distant from the median dorsal line and from the lateral line.

Total length 260 millim.

A single specimen from the north end of Lake Tanganyika.

B. tanganicæ is nearly related to *B.* (*Pelotrophus*) *microlepis* Gthr., from Lake Nyasa. It is distinguished from it by the lesser number of scales between the lateral line and the ventral fin and the greater approximation of the ventral to the anal.

Siluridæ.

12. Chrysichthys myriodon.

Boulenger. Ann. Mus. Congo, Zool. i. p. 139, pl. li. (1900).

Depth of body $4\frac{1}{2}$ times in total length, length of head $3\frac{1}{3}$ to $3\frac{1}{2}$ times. Head broad and much depressed, $\frac{1}{6}$ longer than broad, rough on the vertex and occiput; snout broadly rounded, scarcely projecting beyond the lower jaw, $\frac{1}{3}$ length of head, and twice the diameter of the eye, which is contained 6 times in the length of the head and 2 to $2\frac{1}{2}$ times in the interocular width; the occipital process, which is rough like the occiput, in contact with the interspinous shield; nasal barbel $\frac{3}{4}$ or $\frac{4}{5}$ the diameter of the eye; maxillary barbel a little more than half the length of the head; inner mandibular barbel $\frac{1}{3}$ length of head, outer a little less than half. Vomero-pterygoid teeth very fine and closely set, as are also the præmaxillary and mandibular teeth, forming a broad, horseshoe-shaped, uninterrupted band; its width in the middle a little less than that of the præmaxillary band, but increasing at the sides, where it much exceeds the latter. Dorsal I 6; spine rugose, not serrated, nearly half the length of the head and $\frac{3}{4}$ or $\frac{4}{5}$ the length of the longest soft rays. Adipose dorsal a little longer than deep, its base $\frac{2}{3}$ that of the rayed dorsal and $\frac{1}{3}$ the distance which separates it from the latter. Anal IV 8–9. Pectoral spine a little longer and stronger than the dorsal, feebly striated, and bearing on its inner edge about 20 strong retrorse serræ. Ventral not reaching the anal. Caudal deeply notched, with obtusely pointed lobes; the longest rays measuring double the length of the median. Caudal peduncle $1\frac{2}{3}$ to twice as long as deep. Olive-brown above, white beneath.

Total length 470 millim.

This description is taken from three large specimens—one received from Albertville by the Congo Museum, through Capt. Hecq, one from Tembwi, and one from Kinyamkolo, brought home by Mr. Moore. Compared with specimens of *C. cranchii* of similar size, *C. myriodon* differs by its smaller and more numerous teeth, the greater posterior width of the vomero-pterygoid band, the larger eye, and the more strongly serrated pectoral spine. It has also a higher number of vertebræ (20+27).

Young specimens, measuring up to 130 millim., collected at Kibwesi, in deep water, by Mr. Moore, may, I think, be referred to this species. The depth of the body is 5 or 6 times in the total length; head $\frac{1}{4}$ or $\frac{1}{5}$ longer than broad; diameter of the eye $3\frac{1}{2}$ to $3\frac{2}{3}$ times in the length of the head, $1\frac{1}{4}$ to $1\frac{1}{3}$ in the interocular width; maxillary barbel $\frac{2}{3}$ to $\frac{3}{4}$ the length of the head; vomero-pterygoid teeth forming a narrow subcrescentic band, slightly interrupted mesially. Base of adipose dorsal $\frac{1}{2}$ or $\frac{2}{5}$ its distance from the rayed dorsal; anal IV 8–10; 7 to 9 very large retrorse serræ on the inner side of the pectoral spine. A blackish spot at the end of the dorsal, and another on each lobe of the caudal.

13. Chrysichthys brachynema. (Plate XV.)

Boulenger, Ann. & Mag. N. H. (7) vi. 1900, p. 480.

Depth of body 4 to 5 times in total length, length of head $3\frac{1}{3}$ to $3\frac{1}{2}$ times. Head broad and much depressed, $\frac{1}{5}$ or $\frac{1}{6}$ longer than broad, covered with thick smooth skin; snout much flattened, twice as broad as long, broadly rounded, projecting a little beyond the lower jaw, its length $\frac{1}{3}$ that of the head; diameter of the eye $1\frac{1}{2}$ to twice in the length of the snout, 5 or 6 times in the length of the head, and 2 or $2\frac{1}{2}$ in the interocular width; occipital process hidden under the skin, but reaching the interneural shield; nasal barbel as long as or slightly longer than the diameter of the eye in the young, $\frac{2}{3}$ the diameter of the eye in the adult; maxillary barbel $\frac{1}{2}$ or $\frac{1}{3}$ the length of the head; outer mandibular barbel $\frac{1}{2}$ or $\frac{1}{3}$ the length of the head, inner $\frac{1}{4}$ or $\frac{1}{5}$. Vomero-pterygoid teeth forming a broad crescentic or horseshoe-shaped band, uninterrupted or narrowly interrupted mesially; this band as broad as the præmaxillary band in the adult, also widening behind, narrower and more tapering behind in the young. Dorsal I 6; spine very feebly serrated in front and behind, covered with a thick skin, its length $\frac{2}{5}$ that of the head and a little shorter than the soft rays. Adipose dorsal $1\frac{1}{2}$ to twice as long as deep, its base hardly equal to that of the rayed dorsal and $\frac{1}{3}$ or $\frac{1}{2}$ its distance from the latter. Anal IV 8–9. Pectoral spine thicker and longer than that of the dorsal, armed on its inner side with strong retrorse serræ. Ventral not reaching the anal. Caudal deeply notched, with obtusely pointed lobes, the longest rays twice to twice and a half as long as the middle ones. Caudal peduncle $1\frac{1}{2}$ to $1\frac{2}{3}$ as long as deep. Olive above, white beneath.

Total length 400 millim.

Several specimens from Kalambo and Usambura.

This species is also closely allied to *C. cranchii*, but may be distinguished from it by the absence of rugosities on the skull, the shorter head, and the shorter mandibular barbels.

14. Auchenoglanis biscutatus Geoffr.

Kalambo; also far out, in deep water.

15. Synodontis granulosus. (Plate XVI.)

Boulenger, Ann. & Mag. N. H. (7) vi. 1900, p. 480.

Body feebly compressed, its depth equal to the length of the head and contained 3 to $3\frac{1}{2}$ times in the total length. Head not or but slightly longer than broad, feebly depressed, covered with granular asperities; frontal fontanelle rather narrow; snout rounded, a little more than half the length of the head; eye directed upwards, its diameter $5\frac{1}{2}$ to 6 times in the length of the head, $2\frac{1}{2}$ to $2\frac{2}{3}$ times in the width of the interocular region, which is slightly convex; no occipital keel. Lips moderately developed; maxillary barbel simple, as long as or a little longer than the head, and not extending beyond the anterior third of the pectoral spine; mandibular barbels inserted on a straight transverse line, the outer $\frac{3}{5}$ or $\frac{2}{3}$ the length of the head and thrice that of the inner, both with very short branches, especially near the base, where they are tubercular. Præmaxillary teeth small and numerous, forming a broad band; anterior mandibular teeth small, feebly curved, hardly $\frac{1}{3}$ the diameter of the eye, and numbering 40 to 42. Gill-cleft not extending inferiorly beyond the base of the pectoral fin. Occipito-nuchal shield rugose, tectiform, a little longer than broad, ending in two rounded points which extend to the level of the base of the first soft dorsal ray. Humeral process covered with granular asperities, keeled, narrow, and sharply pointed, extending nearly as far back as the occipito-nuchal shield. The skin of the whole body, including the adipose fin, covered with small, closely-set, granular papillæ. Dorsal I 7; spine rather strong, $1\frac{1}{2}$ times as long as the base of the fin, striated and armed behind with 10 to 15 retrorse serræ. Adipose dorsal 4 times as long as deep, $2\frac{1}{2}$ to $3\frac{1}{2}$ times as long as its distance from the rayed dorsal. Anal III 8. Pectoral spine very strong, as long as that of the dorsal, striated, feebly denticulate on the anterior border, with 15 to 17 strong retrorse serræ on the posterior border. Ventral not reaching anal. Caudal deeply notched. Olive above, yellowish beneath; dorsal, anal, and paired fins black in front, orange behind; caudal black, with a broad orange posterior margin.

Total length 230 millim.

Three specimens from the north end of Lake Tanganyika, in rather deep water.

16. Synodontis multipunctatus Blgr.

Kalambo.

17. Malopterurus electricus Lacép.

Kalambo.

Serranidæ.

18. Lates microlepis Blgr.

Kinyamkolo, and middle of lake, in deep water.

Mr. Moore has satisfied himself that the ferocious fish, over four feet long, attacking

the paddles of boats, to which the late E. J. Glave first drew attention ('Century Magazine,' liii. 1897, p. 902), is no other than the adult of the *Lates* discovered by him, and which was described in the first Report from young specimens.

Cichlidæ.

19. Lamprologus lemairii Blgr.

Specimens obtained at Kibwesi and at Msambu show this fish to grow to a length of 230 millim. It is by far the largest species of the genus.

20. Lamprologus furcifer Blgr.

Msambu.

21. Paratilapia vittata. (Plate XVIII. fig. 1.)

Bouleng. Ann. & Mag. N. H. (7) vii. 1901, p. 1.

Depth of body $3\frac{1}{3}$ to $3\frac{1}{2}$ times in total length, length of head $2\frac{2}{3}$ to 3 times. Profile of snout convex; lower jaw projecting beyond the upper; diameter of eye $1\frac{1}{2}$ to $1\frac{2}{3}$ times in length of snout, 4 to $4\frac{3}{4}$ times in length of head, and equal to interocular width; maxillary extending to below anterior border of eye; teeth in 3 or 4 rows, the outer much larger than the others; 3 or 4 series of scales on the cheek; large scales on the opercle. Gill-rakers short, 10 to 12 on lower part of anterior arch. Dorsal XV–XVI 8–9; spines subequal from the seventh or eighth, which measures about $\frac{1}{3}$ length of head and $\frac{2}{3}$ longest soft rays. Pectoral pointed, about $\frac{2}{3}$ length of head. Ventral reaching vent or origin of anal. Anal III 8–9; third spine longest, as long as middle dorsal spines. Caudal feebly emarginate. Caudal peduncle $1\frac{1}{2}$ times as long as deep. Scales with finely denticulate border, 33–35 $\frac{4}{11-12}$; lat. l. $\frac{20-21}{10-13}$. Olive above, whitish beneath; a blackish stripe on each side above the upper lateral line, and a second from the opercle to the root of the caudal fin, passing over the lower lateral line; dorsal, anal, and caudal fins greyish or blackish, ventrals black in the males.

Total length 120 millim.

Several specimens from Lake Kivu.

22. Paratilapia aurita. (Plate XIX. fig. 2.)

Bouleng. *l. c.* p. 2.

Depth of body 3 to $3\frac{1}{4}$ times in total length, length of head $3\frac{1}{4}$ to $3\frac{1}{2}$ times. Snout short, as long as or a little shorter than the eye, with slightly curved upper profile; lower jaw not projecting beyond the upper; diameter of eye $3\frac{1}{4}$ to $3\frac{3}{4}$ times in length of head, equal to or greater than interocular width; maxillary extending to below anterior fourth or third of eye; teeth in 2 or 3 rows, the outer much larger than the others; 4 or 5 series of scales on the cheek; large scales on the opercle. Gill-rakers

short, 10 or 11 on lower part of anterior arch. Dorsal XV–XVII 9–10; spines increasing in length to the last, which is a little less than half length of head; the longest soft rays produced into filaments, and only a little shorter than head. Pectoral pointed, as long as head. Ventral produced in a filament, and extending to vent or beyond. Anal III 8; third spine stronger and shorter than the last dorsal spine. Caudal feebly emarginate. Caudal peduncle $1\frac{1}{2}$ times as long as deep. Scales with finely denticulate border, 35–36 $\frac{3-4}{9-10}$; lat. l. $\frac{22-25}{14-18}$. Brownish, with or without oblique cross-bars of mother-of-pearl or silvery white, sometimes with ill-defined dark bars across the back; a very distinct, blue-black, opercular spot; dorsal and anal grey or blackish, often striated or spotted with white; the membrane between the dorsal spines edged with black; anal sometimes blackish.

Total length 130 millim.

Numerous specimens from Msambu.

23. Paratilapia bloyeti Sauvage.

Lake Kivu. I have compared the specimens brought home by Mr. Moore with one of the type specimens from Kandoa, Usagara, German East Africa.

24. Paratilapia calliura. (Plate XIX. fig. 3.)

Bouleng. Ann. & Mag. N. H. (7) vii. 1901, p. 2.

Depth of body 4 to $4\frac{1}{2}$ times in total length, length of head 3 to $3\frac{1}{3}$ times. Snout pointed, with straight upper profile, as long as or a little shorter than the eye, the diameter of which is double the interocular width and is contained 3 to $3\frac{1}{3}$ times in length of head; lower jaw projecting beyond the upper; maxillary extending to below anterior fourth of eye; teeth small, in two rows; 2 or 3 series of scales on the cheek; large scales on the opercle. Gill-rakers moderately long, 15 on lower part of anterior arch. Dorsal XVI–XVII 10; spines increasing in length to the last, which measures $\frac{2}{5}$ or $\frac{1}{2}$ length of head; longest soft rays $\frac{2}{3}$ or $\frac{3}{4}$ length of head. Pectoral pointed, a little shorter than head. Ventral reaching vent. Anal III 7–8; third spine longest, a little shorter than last dorsal spine. Caudal feebly emarginate. Caudal peduncle $1\frac{1}{2}$ times as long as deep. Scales with finely denticulate border, 37–40 $\frac{2-3}{9-10}$; lat. l. $\frac{25-29}{13-17}$. Pale brownish above, silvery beneath; a blackish opercular spot; dorsal and anal edged with black; 4 or 5 black bars across the caudal; young with black bars across the dorsal.

Total length 110 millim.

Several specimens from Kalambo.

25. Paratilapia stenosoma. (Plate XVII. fig. 1.)

Bouleng. Ann. & Mag. N. H. (7) vii. 1901, p. 2.

Body very strongly compressed, its depth equal to the length of the head and

contained $2\frac{3}{4}$ to 3 times in total length. Profile of snout descending in a straight or slightly convex line; lower jaw projecting beyond the upper; diameter of eye nearly equal to length of snout or interocular width, $3\frac{1}{3}$ to $3\frac{1}{2}$ times in length of head; maxillary not extending to below anterior border of eye; teeth small, in 2 or 3 rows, the outer very slightly larger than the others; 2 series of scales on the cheek; very thin scales on the opercle. Gill-rakers rather long and closely set, 19 to 23 on lower part of anterior arch. Dorsal XV 13; last spine longest, $\frac{2}{5}$ length of head; soft rays longer, sometimes produced into filaments. Pectoral pointed, a little shorter than head. Ventral reaching vent. Anal III 12–13; third spine longest, a little stronger but shorter than last dorsal spine. Caudal deeply emarginate. Caudal peduncle nearly twice as long as deep. Scales without marginal denticulation, 60–68 $\frac{6}{16}$; lat. l. $\frac{54-58}{31-34}$. Brownish above, silvery beneath, with or without blackish spots and longitudinal bands; dorsal blackish at the end.

Total length 220 millim.

Several specimens from Maswa and from the south end of Lake Tanganyika.

26. Paratilapia leptosoma Blgr.

Msambu.

27. Paratilapia nigripinnis. (Plate XIX. fig. 1.)

Boulenger. Ann. & Mag. N. H. (7) vii. 1901, p. 3.

Depth of body 4 times in total length, length of head 3 to $3\frac{1}{4}$ times. Snout with straight upper profile, as long as diameter of eye, which equals interocular width and is contained $3\frac{1}{3}$ times in length of head; mouth extremely protractile; maxillary extending to below anterior border of eye; teeth very small, in 3 rows; 2 or 3 series of scales on the cheek; opercle covered with scales. Gill-rakers long and thin, closely set, 20 on lower part of anterior arch. Dorsal XV–XVII 11; spines increasing in length to the last, which measures $\frac{2}{5}$ length of head; soft rays longer. Pectoral pointed, as long as head. Ventral reaching origin of anal or beyond. Anal III 8–9; third spine as long as the last dorsal. Caudal deeply emarginate, the lobes produced into filaments. Caudal peduncle twice as long as deep. Scales with denticulate border, 39–40 $\frac{3}{11}$; lat. l. $\frac{29-30}{13-16}$. Dark brown, lighter beneath; fins blackish, the caudal edged with white above and beneath.

Total length 80 millim.

Several specimens from Msambu.

This species is very closely allied to the preceding, but is distinguished by the number of rays in the dorsal and anal fin (D. XV–XVII 11, A. III 8–9, instead of D. XII–XIV 14–16, A. III 10–12).

28. Bathybates ferox Blgr.

Several specimens from the South and West Coasts, from Kalambo, and from Usambura. I have also examined specimens from Moliro and Albertville. The species is thus seen to be widely dispersed in the lake, and not confined to great depths.

29. Bathybates fasciatus. (Plate XVII. fig. 2.)

Bouleng. Ann. & Mag. N. H. (7) vii. 1901, p. 3.

Depth of body $4\frac{1}{3}$ times in total length, length of head $3\frac{1}{2}$ times. Shape of head similar to that of the preceding species, but eye smaller, its diameter about twice in length of snout, 5 times in length of head, and $1\frac{1}{2}$ in interocular width; 8 series of small scales on the cheek; larger scales on the opercle. 18 gill-rakers on lower part of anterior arch. Dorsal XVII 16; spines subequal from the fifth, which measures $\frac{1}{4}$ length of head; longest soft rays $\frac{1}{3}$ length of head. Pectoral pointed, $\frac{2}{3}$ length of head. Ventral not half as long as the distance between its base and the vent. Anal III 18; spines very weak. Caudal forked. Caudal peduncle twice and a half as long as deep. Scales very small, 140 in a longitudinal series above the upper lateral line, $\frac{11}{25}$ in a transverse series; lat. l. $\frac{75}{45}$. Brownish above, white beneath; a series of large, rounded, blackish spots on each side of the back above the lateral line, alternating with a series of vertical blackish bars on each side of the body; on the tail, from the middle of the soft dorsal, the spots unite into a band which extends to the caudal, and the vertical bars likewise fuse to form a lateral band; a blackish spot on the opercle, another at the base of the ventral; two black bands on the dorsal, a basal and a marginal.

Total length 340 millim.

A single specimen from the West Coast, at Tembwi.

This second species of the remarkable genus *Bathybates* differs from its congener in the smaller eye, the more numerous gill-rakers, and the smaller scales.

30. Pelmatochromis polylepis.

Bouleng. Ann. Mus. Congo, Zool. i. p. 143, pl. lii. fig. 1 (1900).

Depth of body $2\frac{1}{2}$ to $2\frac{2}{3}$ times in total length, length of head 3 to $3\frac{1}{3}$ times. Snout with straight upper profile, $1\frac{1}{3}$ times diameter of eye, very deep, its length not exceeding the width of the præorbital region; diameter of eye $3\frac{1}{2}$ to $3\frac{2}{3}$ times in length of head, equal to or a little greater than interocular width; maxillary extending nearly to below anterior border of eye; teeth very small, in 4 or 5 irregular rows in both jaws, the outer somewhat larger; 4 or 5 series of scales on the cheek; larger scales on the opercle. Gill-rakers short, lamellar, denticulate, 14 or 15 on lower part of anterior arch. Dorsal XV–XVI 14–15; spines subequal from the sixth, which measures $\frac{2}{5}$ or

a little more than $\frac{1}{3}$ length of head. Pectoral pointed, falciform, at least as long as head. Ventral reaching vent, the outer ray produced into a filament. Anal III 8; third spine much stronger than dorsal spines, nearly $\frac{1}{2}$ length of head. Caudal rather deeply emarginate. Caudal peduncle a little longer than deep. Scales with denticulate border, 55–58 $\frac{6-7}{18}$; lat. l. $\frac{25-31}{47-48}$, the upper extending to below the last spines or the first soft rays of the dorsal, the lower originating a little behind the shoulder and extending to the caudal fin. Body golden, olive on the back; purplish streaks along the dorsal and caudal fins, sometimes forming a wide-meshed network.

Total length 300 millim.

This species was discovered almost simultaneously by Mr. Moore at Kinyamkolo and Kibwesi, and by Capt. Hecq, of the Congo Free State, at Albertville.

The genus *Pelmatochromis* had not yet been recorded from Lake Tanganyika. *P. polylepis* is very closely allied to *P. lateralis* Blgr., from the Congo; it differs in its much smaller scales.

31. Ectodus longianalis Blgr. (Plate XIX. fig. 4.)

Several specimens from the north end of Lake Tanganyika, near Usambura.

The females, measuring 95 millim., contain ripe ova, the diameter of which is 2 millim. In the adult male (115 millim.) the upper surface of the snout, the chin, the middle of the throat, the dorsal and anal fins, and the extremity of the ventrals are black; a few large, black, white-edged ocelli on the spinous dorsal, along which runs a white line, which is also present on the soft dorsal and on the anal; oblique white lines on the soft dorsal; large, round, white spots on the ventrals [1]; two crescentic bands on the caudal, the first grey, the second, marginal, blackish.

The specimens brought home by Mr. Moore have enabled me to make an examination of the skeleton, which differs very considerably from that of *Paratilapia*. Three very low crests, supra-occipital and parietal, extend forwards to between the orbits. The precaudal vertebræ are much fewer than the caudals, 14 of the former as against 24 of the latter, a character, quite exceptional among the *Cichlidæ*, shared by the genera *Xenotilapia* and *Trematocara*; the ribs are inserted on the parapophyses, the last pair of which form a hæmal arch.

32. Xenotilapia ornatipinnis. (Plate XVIII. fig. 2.)

Bouleng. Ann. & Mag. N. H. (7) vii. 1901, p. 3.

Depth of body nearly equal to length of head, $3\frac{1}{3}$ to $3\frac{1}{2}$ times in total length. Head quite similar to that of *X. sima*. 15 to 17 gill-rakers on lower part of anterior arch. Dorsal XIII–XV 12–13; spines subequal from the 5th or 6th, $\frac{2}{5}$ length of head.

[1] In this genus the inner rays of the ventral are the longest.

Pectoral pointed, as long as or a little longer than the head. Ventral not reaching anal [1]. Anal III 7–8; third spine $\frac{2}{5}$ length of head. Caudal deeply notched, crescentic. Caudal peduncle $1\frac{2}{3}$ times as long as deep. Scales with denticulate border, 34–37 $\frac{3}{10}$; lat. l. $\frac{28\text{-}32}{13\text{-}18}$ $\frac{}{4\text{-}12}$. Pale brownish; a more or less distinct silvery lateral band; spinous dorsal black-edged; large blackish spots or oblique bars on the dorsal; upper lobe of caudal edged with blackish; a chevron-shaped blackish band lower down on the caudal, disposed asymmetrically.

Total length 110 millim.

Several specimens from Kibwesi.

This species is easily distinguished from *X. sima* by the shorter body, the fewer anal rays, and the lower number of scales in a longitudinal series.

The skeleton of *Xenotilapia* is very similar to that of *Ectodus*. There are likewise three low crests on the back of the skull, the vertebræ number 13+22 in *X. sima*, 14+20 in *X. ornatipinnis*, and the ribs are remote from the centres.

33. Trematocara marginatum Blgr.

Usambura market.

34. Trematocara unimaculatum. (Plate XVIII. fig. 3.)

Boulenger. Ann. & Mag. N. H. (7) vii. 1901, p. 3.

Depth of body 3 to $3\frac{1}{2}$ times in total length, length of head $2\frac{2}{3}$ to $2\frac{3}{4}$ times. Snout with curved upper profile, as long as or a little shorter than the eye, the diameter of which is nearly double interorbital width and contained 3 to $3\frac{1}{4}$ times in length of head; mouth extending to below anterior border of eye; cheek naked; a few deciduous scales on opercle; nasal, frontal, præorbital, suborbital, præopercular, and mandibular bones cavernous, with large cavities covered with thin skin and separated by narrow septa. Gill-rakers short, 17 on lower part of anterior arch. Dorsal X–XII 9–11; spines increasing in length to the 6th or 7th, which measures $\frac{1}{2}$ length of head; soft rays scarcely longer. Pectoral very pointed, as long as or a little longer than the head. Ventral reaching origin of anal. Anal III 7–8; third spine nearly as long as dorsals. Caudal deeply notched, crescentic. Caudal peduncle nearly twice as long as deep. Scales 30–32 $\frac{3}{7}$; lat. l. 5–14. Silvery, brownish above; a large, rounded, black spot on posterior third of spinous part of dorsal, rarely followed by a second.

Total length 120 millim.

Several specimens from the Usambura market.

[1] As in *Ectodus* the inner rays of the ventral are the longest.

Closely allied to the preceding species. Differing in the longer dorsal spines, fewer anal rays, and in the presence of a black spot on the dorsal.

I have been able to examine the skeleton of this species. The occipital crest is strong and extends to between the orbits; a more feeble parietal crest. The median pharyngeal teeth have rounded spheroidal crowns. 12 præcaudal and 19 caudal vertebræ; the last præcaudal vertebra bears a hæmal arch. It is not without interest to point out the parallelism that can be drawn in comparing *Trematocara* (with its excessively developed cephalic cavities) with the perch-like *Cichla* on the one hand and *Acerina* and *Perca*, among *Percidæ*, on the other:—

Trematocara:	Vert. 12+19=31.	*Acerina*:	Vert. 15+19=34.
Cichla:	Vert. 18–19+17=35–36.	*Perca*:	Vert. 21–22+19–21=41–42.

The two genera in each family standing very nearly in the same relation to each other both as regards the skull and the vertebral column.

35. Telmatochromis temporalis Blgr.

Kibwesi.

Gephyrochromis.

Bouleng. Ann. & Mag. N. H. (7) vii. 1901, p. 4.

A band of very small tricuspid teeth in each jaw, with an outer series of larger conical teeth bent inwards; lateral teeth conical. Maxillary exposed. Body moderately elongate; scales cycloid; two lateral lines. Dorsal with 17 spines, anal with 3.

Differs from *Paratilapia* as *Telmatochromis* differs from *Lamprologus*.

36. Gephyrochromis moorii. (Plate XX. figs. 1, 1 *a*.)

Bouleng. *l. c.*

Depth of body equal to length of head, 3 times in total length. Snout with slightly convex upper profile, as long as the diameter of the eye, which is contained $3\frac{1}{3}$ times in length of head and equals interocular width; maxillary extending to between nostril and eye; 56 conical teeth, with brown points, in the upper jaw; 3 series of scales on the cheek; larger scales on the opercle. Gill-rakers short, 13 on lower part of anterior arch. Dorsal XVII 8; spines increasing in length to the last, which measures $\frac{2}{5}$ length of head and $\frac{2}{5}$ longest soft rays. Pectoral nearly as long as head. Ventral produced into a long filament extending beyond origin of anal. Anal III 7; third spine longest, a little shorter than last dorsal spine. Caudal rounded. Caudal peduncle as long as deep. Scales 30 $\frac{3}{11}$; lat. l. $\frac{22}{13}$. Uniform pale brown.

Total length 120 millim.

A single specimen from the north end of Lake Tanganyika.

37. Simochromis diagramma Gthr.

Msambu.

38. Tilapia nilotica L.

This Nile species, which is also found in Syria, in the Senegal, Gambia, and Niger, has been found in Lake Kivu.

39. Tilapia burtoni Gthr.

Discovered at Ujiji by Mr. Coode Hore, this species has since been found at Albertville by Capt. Hecq. Mr. Moore obtained specimens in Lake Kivu.

40. Tilapia dardennii Blgr.

Kibwesi and Kalambo. Grows to a length of 230 millim.

41. Tilapia labiata Blgr.

Kibwesi.

42. Tilapia pleurotænia. (Plate XVIII. fig. 4.)

Boulenger, Ann. & Mag. N. H. (7) vii. 1901, p. 4.

Depth of body $2\frac{1}{2}$ to 3 times in total length, length of head 3 to $3\frac{1}{2}$ times. Snout with the profile descending in a straight line, as long as the diameter of the eye, which is contained $3\frac{1}{3}$ to $3\frac{1}{2}$ times in length of head, and exceeds a little interocular width; mouth small, its width half, or a little more than half, that of the head, extending to below nostril or between nostril and eye; teeth very small, in 3 series, outer bicuspid; 3 or 4 series of scales on the cheek. Gill-rakers short, 10 to 12 on lower part of anterior arch. Dorsal XV–XVIII 11–12; last spine longest, a little less than half length of head; longest soft rays $\frac{2}{3}$ length of head. Pectoral pointed, a little shorter than the head, not quite reaching origin of anal. Anal III 8–10; third spine a little shorter than last dorsal spine. Caudal deeply notched, crescentic. Caudal peduncle $1\frac{1}{2}$ as long as deep. Scales very thin, without denticulation, 32–35 $\frac{4}{11-12}$; lat. l. $\frac{22-24}{10-15}$. Pale brown above, white beneath; a blackish lateral stripe, from the opercle to the caudal; fins greyish; small, round, white spots on soft dorsal and caudal.

Total length 110 millim.

Several specimens from the north end of Lake Tanganyika and from the mouth of the Rusisi River.

43. Tilapia trematocephala. (Plate XIX. fig. 6.)

Boulenger, Ann. & Mag. N. H. (7) vii. 1901, p. 4.

Depth of body equal to length of head, $3\frac{1}{4}$ times in total length. Snout with slightly convex upper profile, a little shorter than diameter of eye, which is contained 3 times in length of head and exceeds interocular width; mouth small, its width half that of head, extending to between nostril and eye; teeth very small, in 2 rows, outer bicuspid; 3 series of scales on the cheek; large scales on the opercle; orifices of sensory canals

on head remarkably large. Gill-rakers rather short, 13 on lower part of anterior arch. Dorsal XVI 11; last spine longest, half length of head; longest soft rays produced into filaments, half length of head. Pectoral pointed, $\frac{3}{4}$ length of head, not reaching origin of anal. Ventral produced into a filament, extending beyond origin of anal. Anal III 9; third spine as long as and stronger than last dorsal spine; some of the soft rays produced into filaments, as in the dorsal. Caudal deeply emarginate. Caudal peduncle $1\frac{1}{2}$ as long as deep. Scales very thin, without denticulation, 40 $\frac{3}{10}$; lat. l. $\frac{28}{7}$. Brownish; dorsal and caudal greyish; ventrals and anal black, latter edged with white.

Total length 90 millim.

A single specimen from the north end of Lake Tanganyika.

44. Tilapia boops. (Plate XIX. fig. 5.)

Boulenger, Ann. & Mag. N. H. (7) vii. 1901, p. 5.

Depth of body equal to length of head, $3\frac{1}{4}$ to $3\frac{1}{3}$ times in total length. Snout with strongly convex upper profile, shorter than diameter of eye, which is $2\frac{1}{2}$ times in length of head, and exceeds a little interocular width; mouth $\frac{2}{3}$ width of head, subinferior, not extending quite to below anterior border of eye; teeth very small, tricuspid, in 3 rows; 2 or 3 series of scales on the cheek; large scales on the opercle. Gill-rakers short, 13 on lower part of anterior arch. Dorsal XII–XIII 14; spines slender, equal from the 7th, which measures nearly $\frac{1}{3}$ length of head; soft rays scarcely longer. Pectoral pointed, as long as head, reaching origin of anal. Ventral produced into a filament, extending beyond origin of anal. Anal III 8–9; third spine as long as and stronger than longest dorsal spines. Caudal deeply emarginate, crescentic. Caudal peduncle nearly twice as long as deep. Scales thin, without denticulation, 39–40 $\frac{5}{14\text{-}15}$; lat. l. $\frac{34\text{–}35}{15\text{–}19}$. Brown above, white beneath; a blackish opercular spot.

Total length 90 millim.

Two specimens from Msambu.

45. Tilapia microlepis Blgr.

Kalambo.

This species grows to a length of 440 millim. Such large specimens lose the secondary cusp of the teeth, and might therefore be referred to the genus *Paratilapia*.

46. Petrochromis tanganicæ.

Chromis tanganicæ Günth. Proc. Zool. Soc. 1893, p. 630, fig.

Kalambo.

This species grows to a length of 300 millim. Adult specimens agree entirely in their dentition with *Petrochromis polyodon* Blgr.

Asprotilapia.

Bouleng. Ann. & Mag. N. H. (7) vii. 1901, p. 5.

Teeth small, tricuspid, closely set, in two series in both jaws. Mouth inferior, transverse; greater part of maxillary bone concealed under the præorbital. Body elongate, much attenuate in the caudal region. Scales ctenoid; two lateral lines. Dorsal with 14 spines, anal with 3.

Allied to *Tilapia*. By the form of the body, the type of this genus recalls *Aspro* among the *Percidæ*.

47. Asprotilapia leptura. (Plate XX. figs. 2, 2 *a*, 2 *b*.)

Bouleng. *l. c.*

Body rather feebly compressed, its depth 5 times in total length; length of head 4 times in total length. Snout subconical, strongly projecting beyond the mouth, its length $\frac{1}{3}$ that of the head: eye very large, its diameter equal to length of snout and nearly twice interorbital width, $2\frac{3}{5}$ times in length of head; width of mouth $\frac{3}{5}$ that of head; 36 teeth in the outer row of the upper jaw; 3 series of small scales on the cheek; larger scales on the opercle. Gill-rakers very short, tubercle-like, 15 on lower part of anterior arch. Dorsal XIV 12; spines slender and subequal, $\frac{2}{5}$ length of head; soft rays a little longer. Pectoral pointed, a little shorter than head. Ventral reaching vent. Anal III 8; third spine nearly as long as dorsals. Caudal deeply emarginate, crescentic. Caudal peduncle 3 times as long as deep. Scales strongly denticulate, 38 $\frac{2}{11}$; lat. l. $\frac{27}{20}$. Brown, darker on the snout and vertex; a blackish opercular spot; fins greyish.

Total length 95 millim.

A single specimen from Msambu.

48. Xenochromis hecqui Blgr.

Three specimens from Usambura. Grows to a length of 270 millim. D. XVI–XVII 10–11; A. III 9–10; Sq. 64–67 $\frac{6}{20}$; lat. l. $\frac{53-60}{35-43}$.

Mastacembelidæ.

49. Mastacembelus frenatus. (Plate XX. fig. 3.)

Bouleng. Ann. & Mag. N. H. (7) vii. 1901, p. 5.

Depth of body 13 times in total length, length of head $8\frac{2}{3}$ times. Vent equally distant from end of snout and from caudal fin, separated from head by a space equal to $3\frac{2}{3}$ times length of latter. Snout 3 times length of eye, produced into a trifid appendage, the length of which exceeds a little diameter of eye; buccal cleft extending to below anterior border of eye; no præopercular spines. Dorsal and anal confluent

with caudal, which is short and rounded; dorsal XVIII 85; anal II 90; first anal spine very short, second $\frac{1}{4}$ length of head; distance between first dorsal spine and head $1\frac{2}{3}$ times length of latter. Pectoral $\frac{2}{7}$ length of head. Scales extremely small, 22 between origin of dorsal and lateral line. Yellowish brown above, marbled with darker, yellowish beneath; a dark brown streak on each side of the head, passing through the eye; two brown bars across the caudal.

Total length 250 millim.

A single specimen, a female full of ova, from the north end of Lake Tanganyika.

50. Mastacembelus tæniatus. (Plate XX. fig. 4.)

Bouleng. Ann. & Mag. N. H. (7) vii. 1901, p. 6.

Depth of body 13 times in total length, length of head $6\frac{1}{2}$ times. Vent equally distant from head and from caudal fin, separated from head by a space equal to 3 times length of latter. Snout twice as long as eye, ending in a trifid appendage as long as latter; buccal cleft extending to below anterior border of eye; no præopercular spines. Dorsal and anal fins confluent with caudal, which is short and rounded; dorsal XXXIII 85; anal II 85; first anal spine extremely short, second as long as last dorsal. Pectoral $\frac{1}{5}$ length of head. Scales extremely small, 25 between origin of dorsal and lateral line. Yellowish; a brown lateral band, from the end of the snout, through the eye, to the caudal region, where it widens, its borders become sinuous, and it bears some yellow spots.

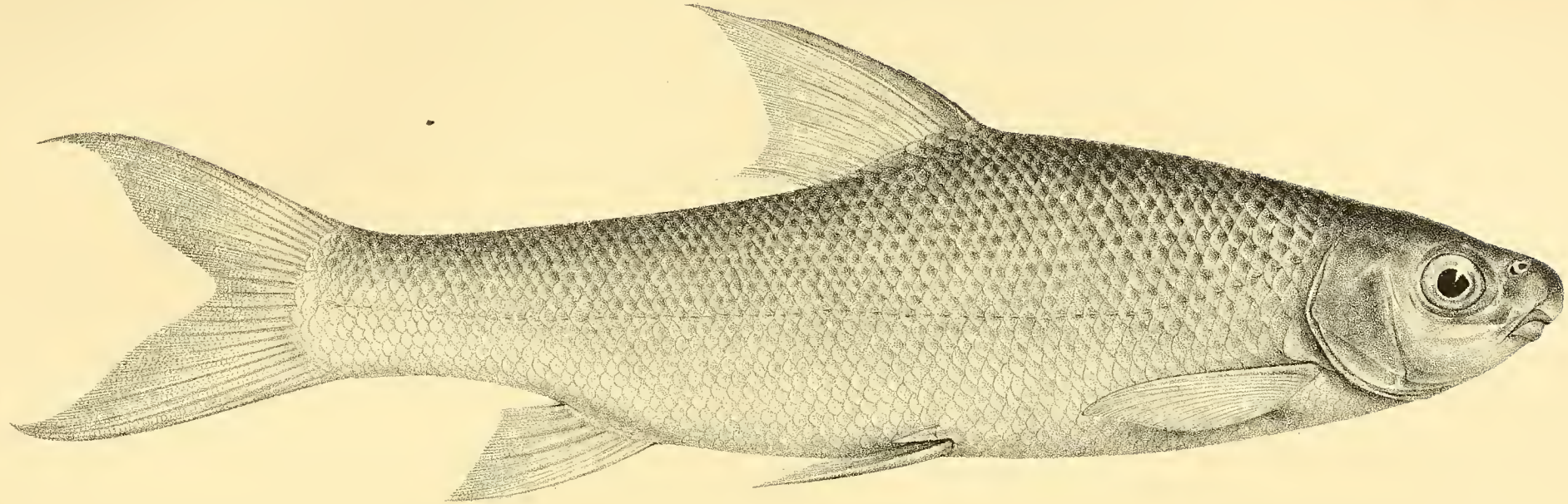
Total length 105 millim.

A single specimen from the north end of Lake Tanganyika.

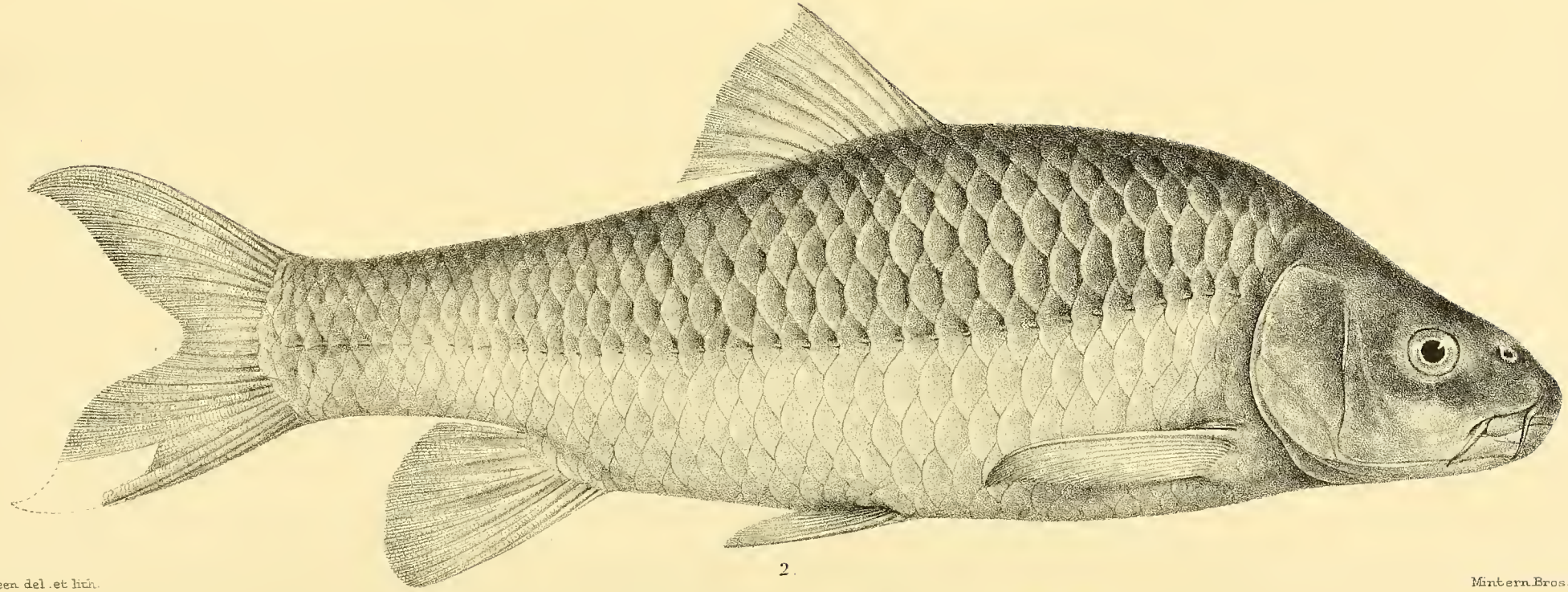
PLATE XII.

PLATE XII.

Fig. 1. *Capoëta tanganicæ*, p. 143. Reduced $\frac{3}{4}$.
Fig. 2. *Barbus platyrhinus*, p. 144. Reduced $\frac{3}{5}$.



1.



2.

J. Green del. et lith.

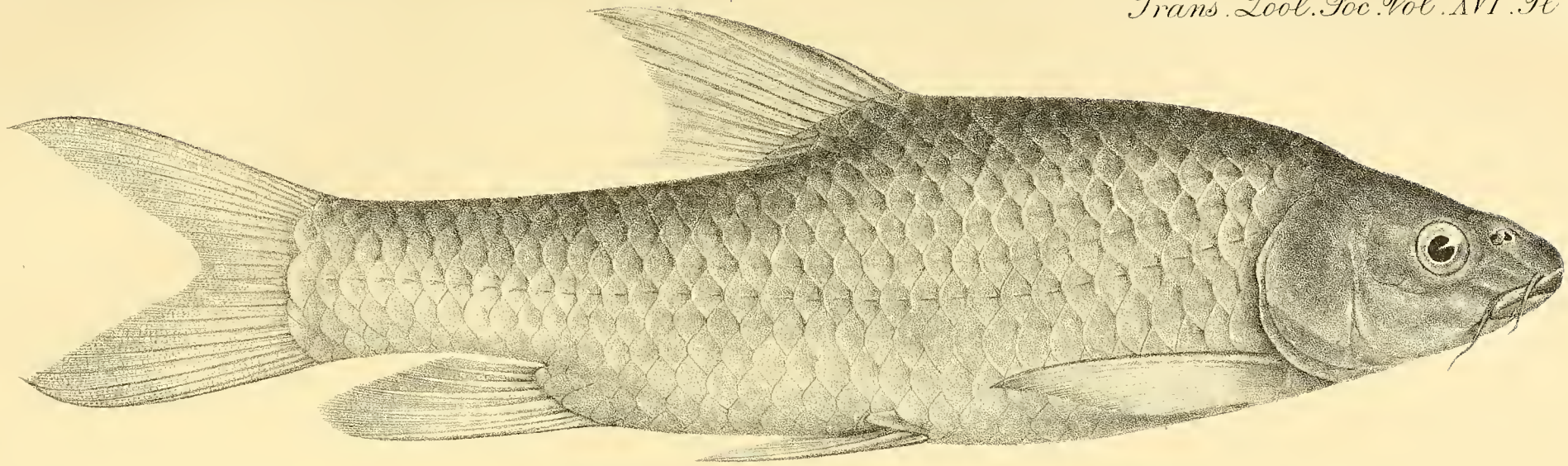
Mintern Bros. imp.

1. CAPOETA TANGANICÆ. 2. BARBUS PLATYRHINUS.

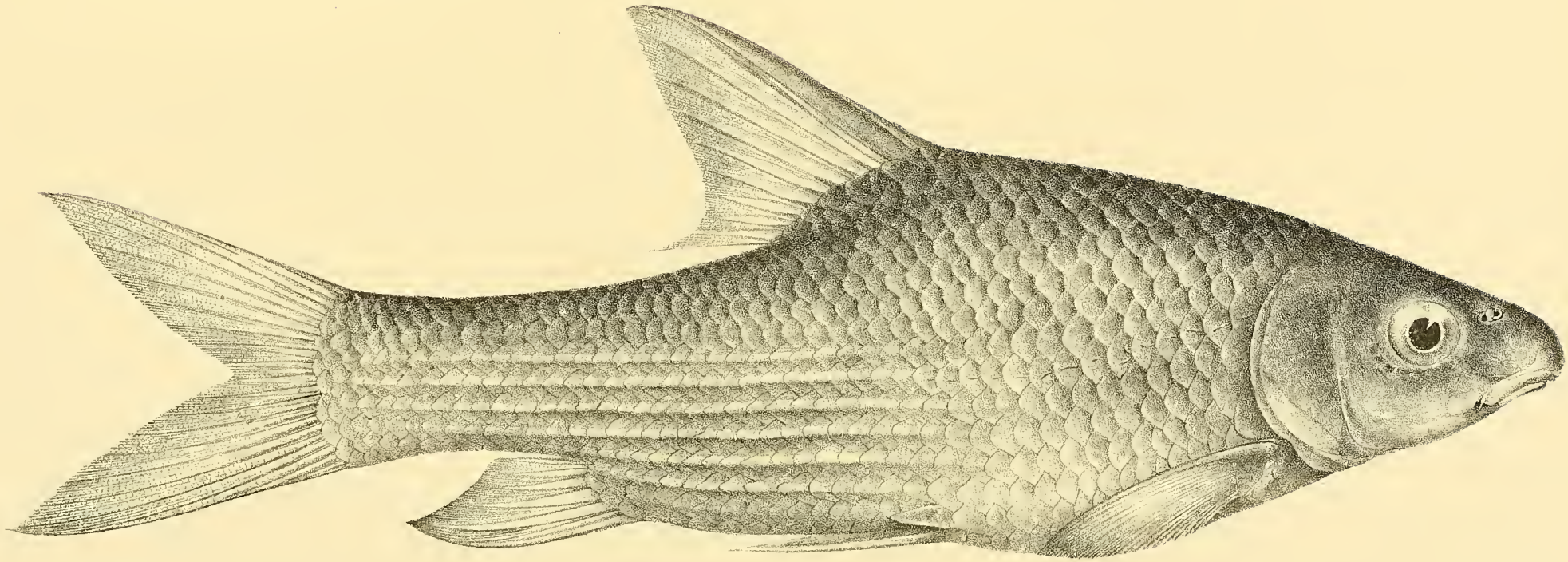
PLATE XIII.

PLATE XIII.

Fig. 1. *Barbus altianalis*, p. 144. Reduced $\frac{7}{11}$.
Fig. 2. ,, *tropidolepis*, p. 145. Reduced $\frac{3}{4}$.



1.



2.

J. Green del. et lith.

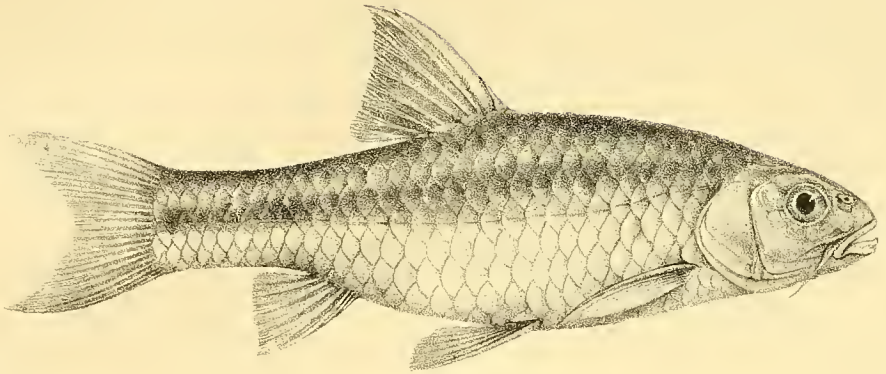
Mintern Bros imp.

1. BARBUS ALTIANALIS. 2. BARBUS TROPIDOLEPIS.

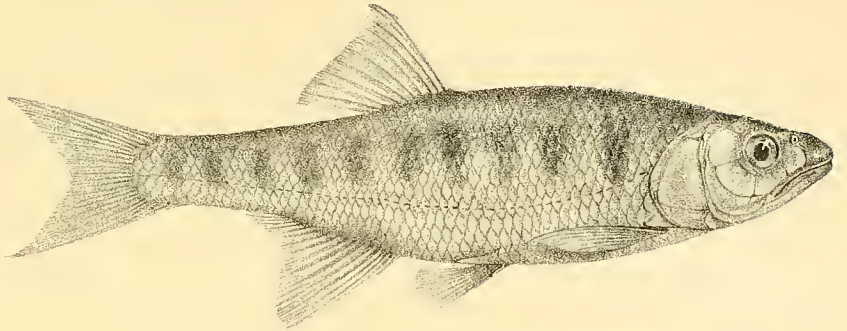
PLATE XIV.

PLATE XIV.

Fig. 1. *Barbus serrifer*, p. 145. Reduced $\frac{6}{7}$.
Fig. 2. *Barilius moorii*, p. 146. Reduced $\frac{9}{10}$.
Fig. 2 *a*. „ „ Upper view of head. × 2.
Fig. 3. „ *tanganicæ*, p. 146. Reduced $\frac{7}{9}$.
Fig. 3 *a*. „ „ Upper view of head. Nat. size.



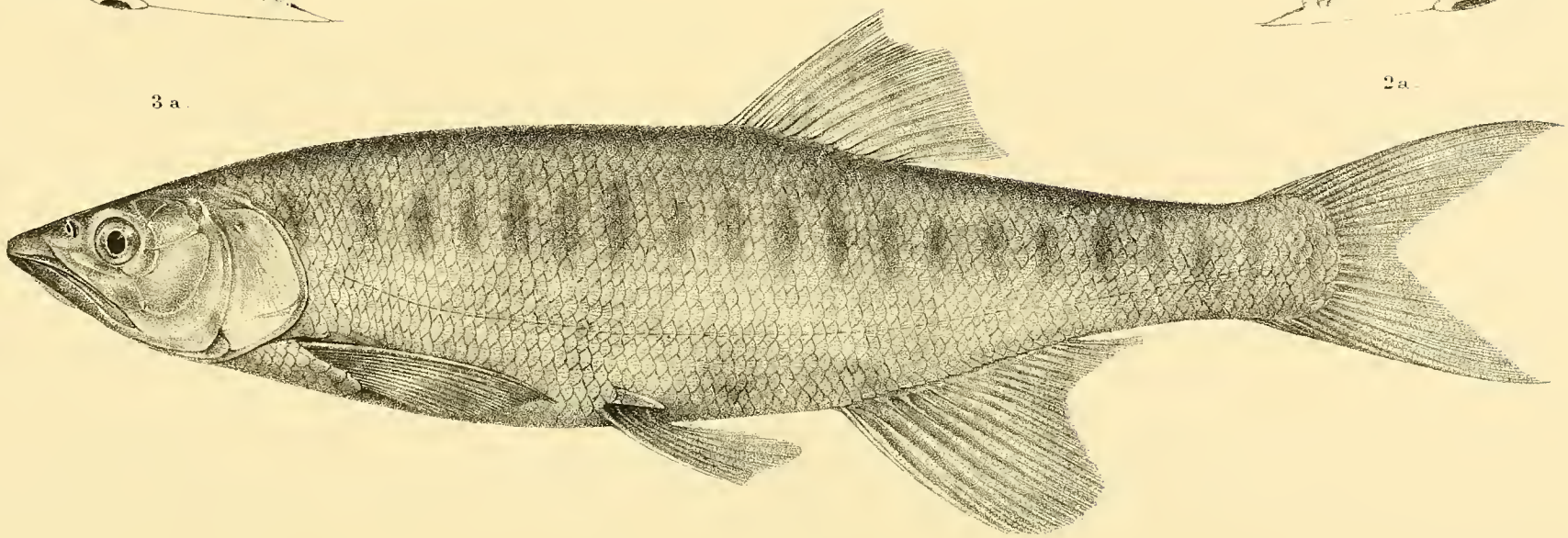
1.



2.

3a.

2a.



3.

J. Green del. et lith.

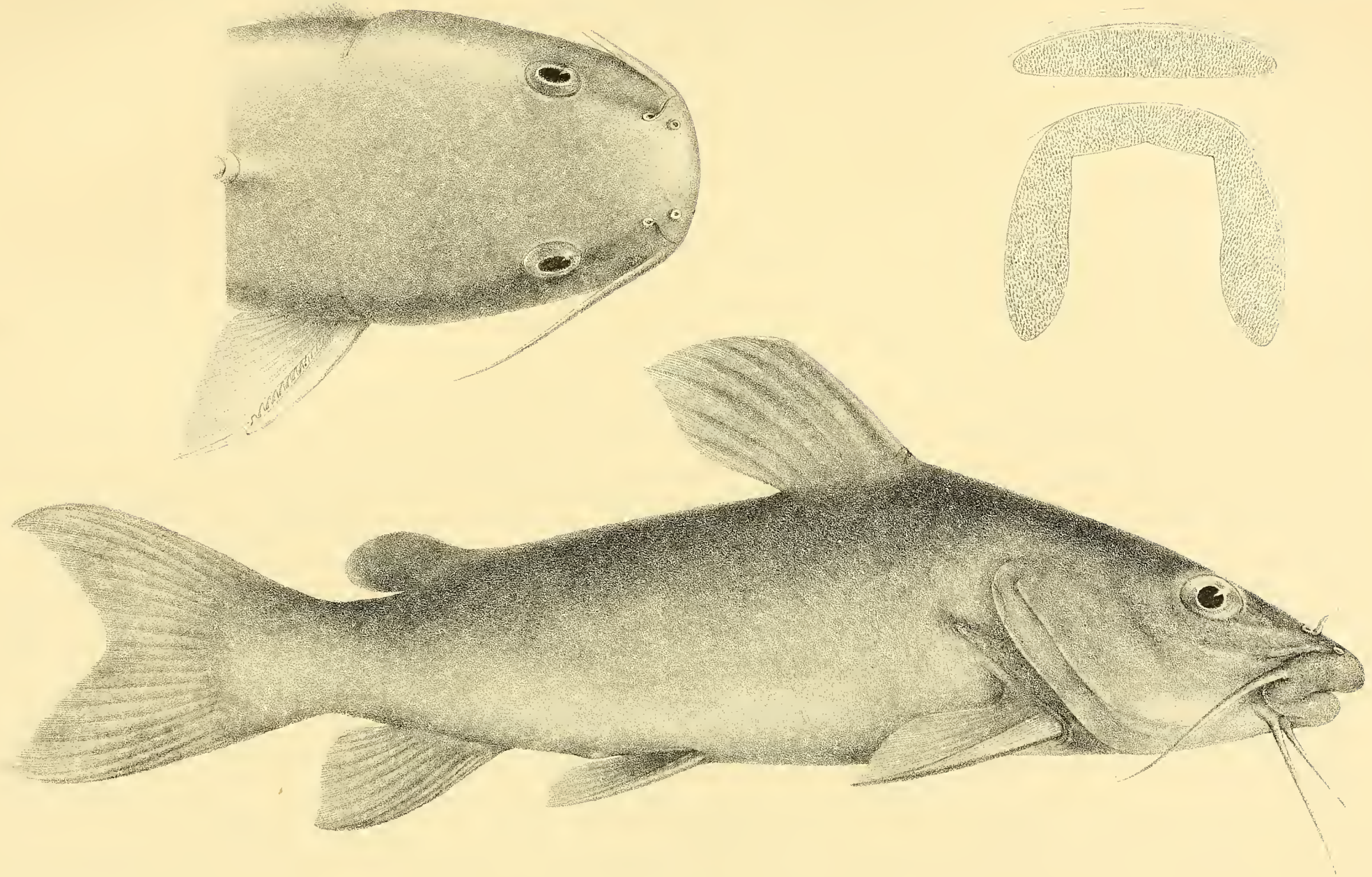
Mintern Bros. imp.

1. BARBUS SERRIFER. 2. BARILIUS MOORII. 3. BARILIUS TANGANICÆ

PLATE XV.

PLATE XV.

Chrysichthys brachynema, p. 148, with upper view of head, reduced $\frac{5}{9}$; and dentition of upper jaw and palate, nat. size.



J. Green del. et lith.

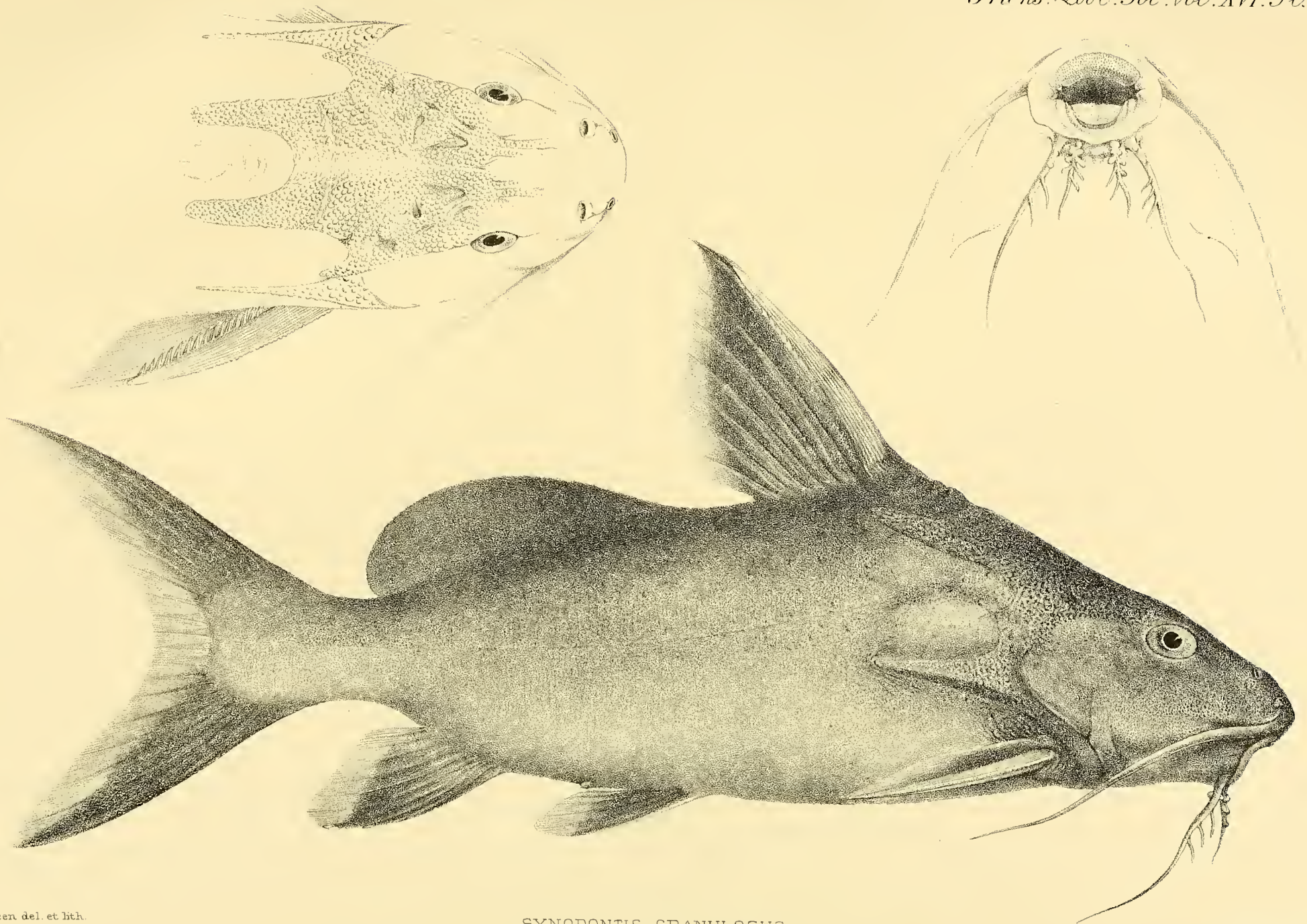
CHRYSICHTHYS BRACHYNEMA.

Mintern Bros. imp.

PLATE XVI.

PLATE XVI.

Synodontis granulosus, p. 149, with upper and lower views of head.



J. Green del. et lith.

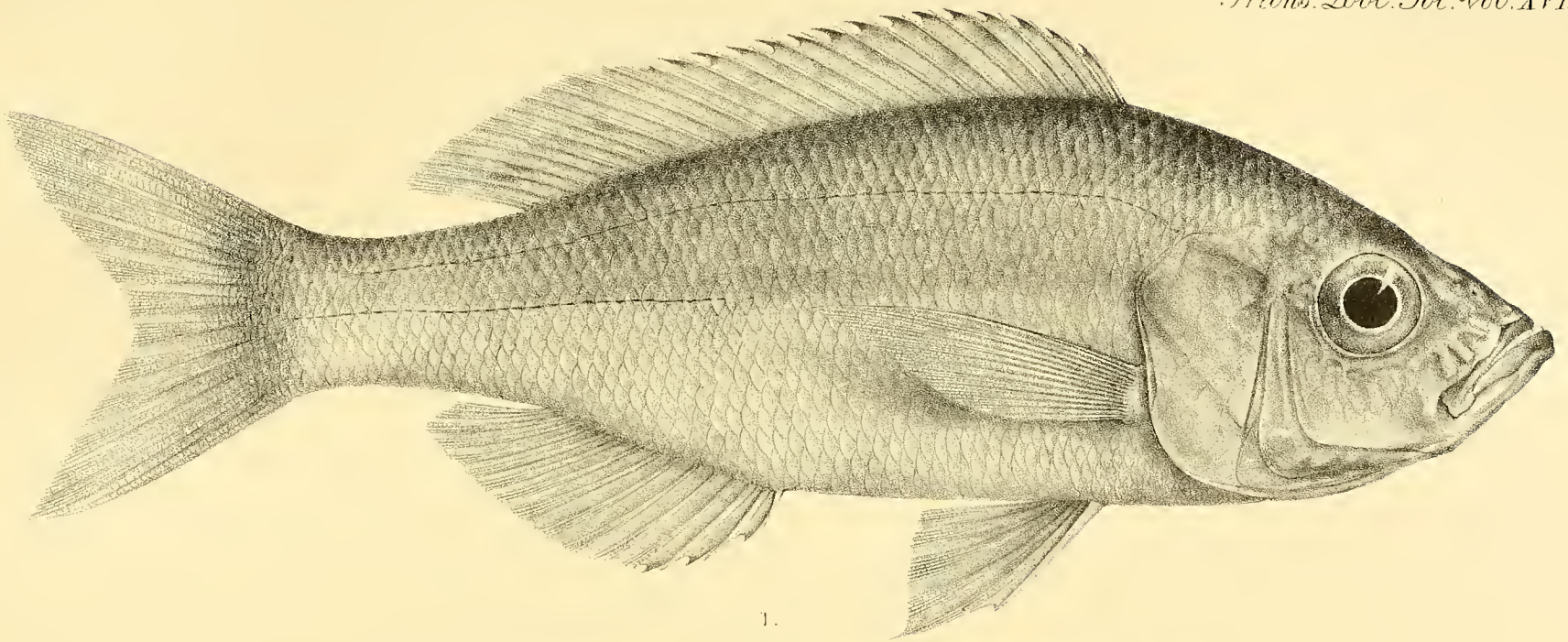
SYNODONTIS GRANULOSUS.

Mintern Bros. imp

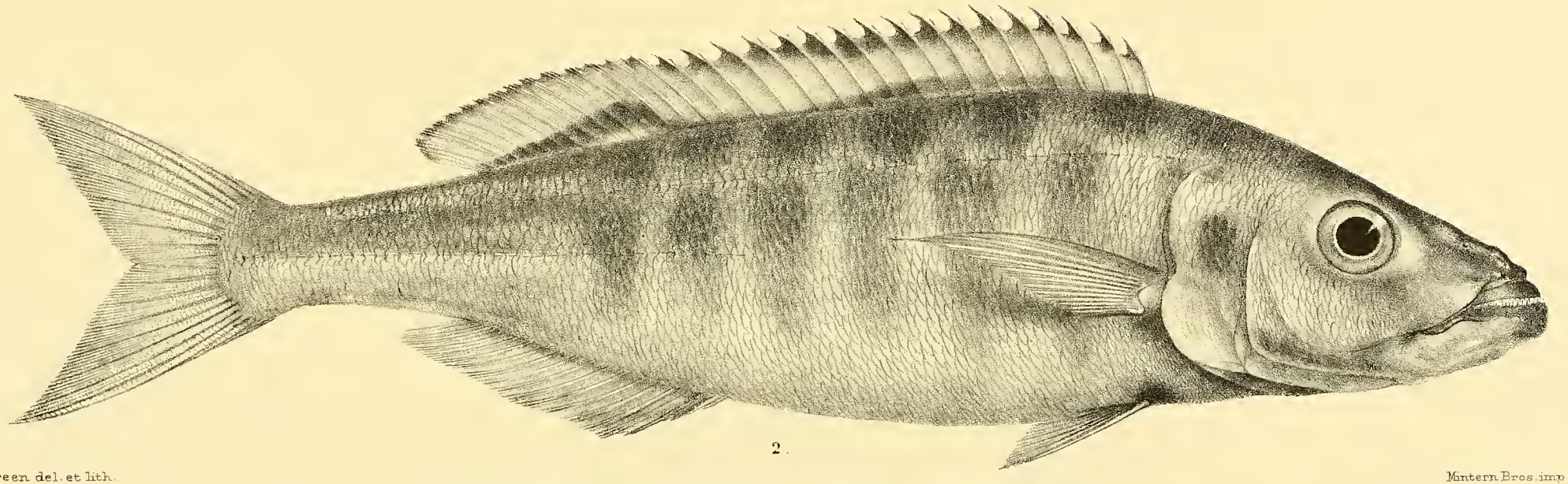
PLATE XVII.

PLATE XVII.

Fig. 1. *Paratilapia stenosoma*, p. 151.
Fig. 2. *Bathybates fasciatus*, p. 153. Reduced $\frac{2}{3}$.



1.



2.

J. Green del. et lith.

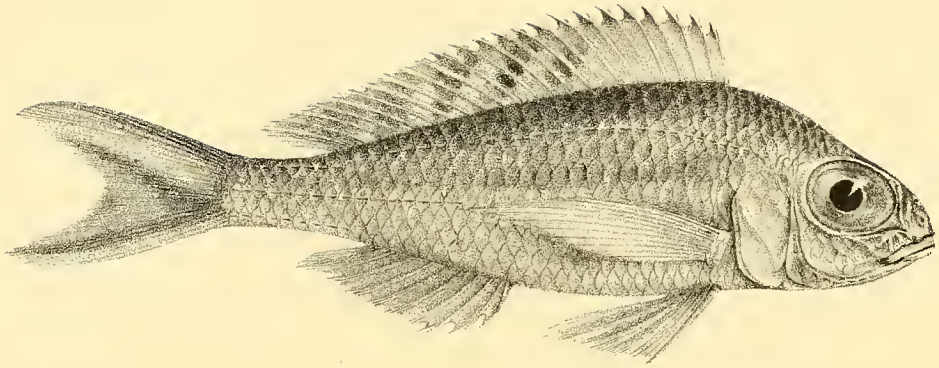
Mintern Bros. imp.

1. PARATILAPIA STENOSOMA. 2. BATHYBATES FASCIATUS.

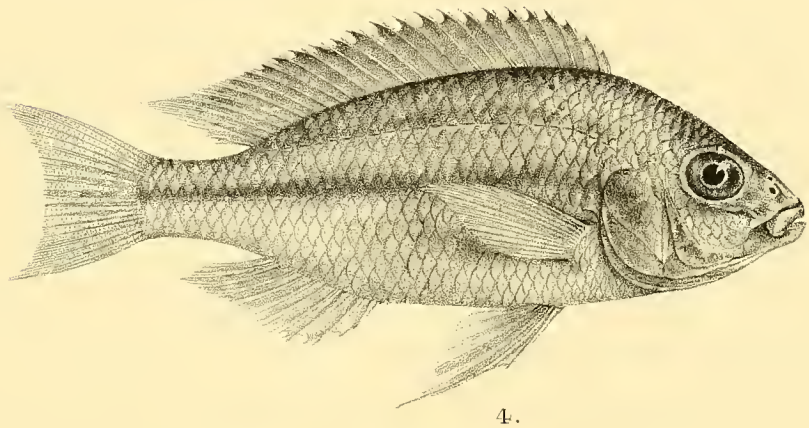
PLATE XVIII.

PLATE XVIII.

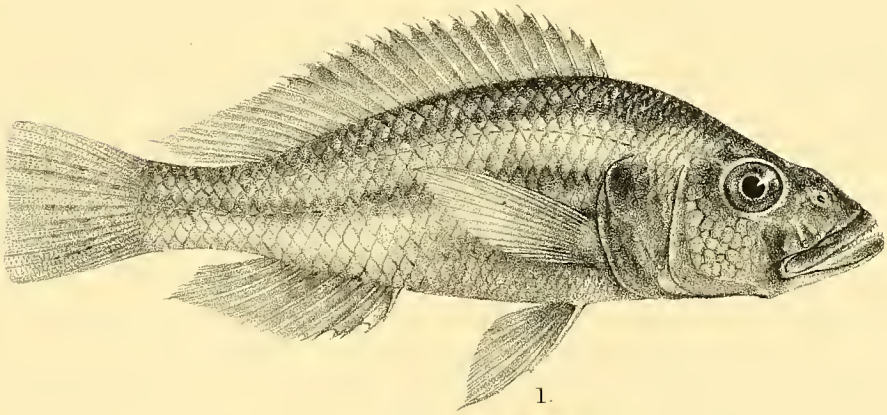
Fig. 1. *Paratilapia vittata*, p. 150.
Fig. 2. *Xenotilapia ornatipinnis*, p. 154.
Fig. 3. *Trematocara unimaculatum*, p. 155.
Fig. 4. *Tilapia pleurotænia*, p. 157.



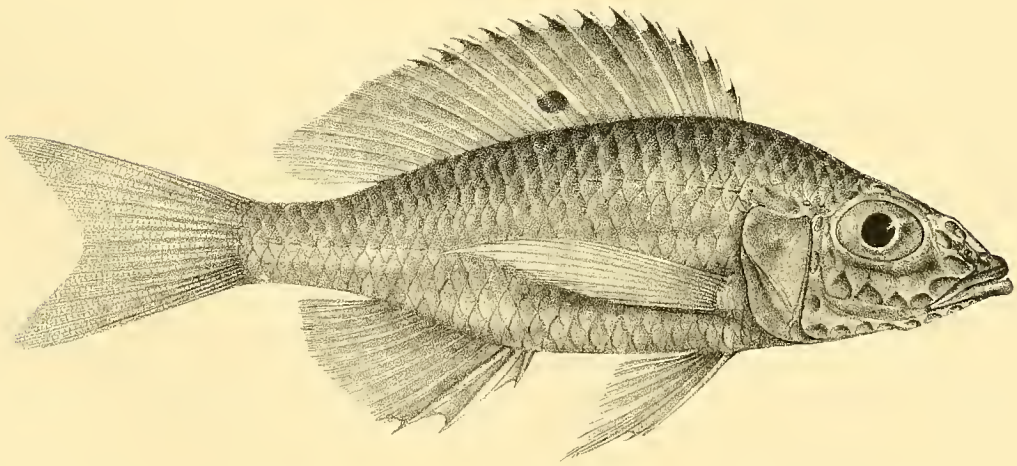
2.



4.



1.



3.

J. Green del. et lith.

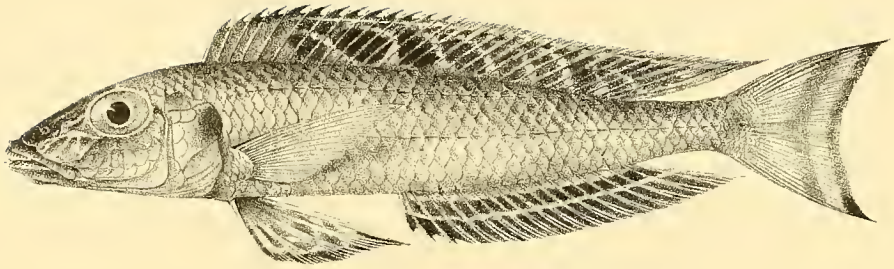
Mintern Bros imp.

1. PARATILAPIA VITTATA. 2. XENOTILAPIA ORNATIPINNIS.
3. TREMATOCARA UNIMACULATUM. 4. TILAPIA PLEUROTÆNIA.

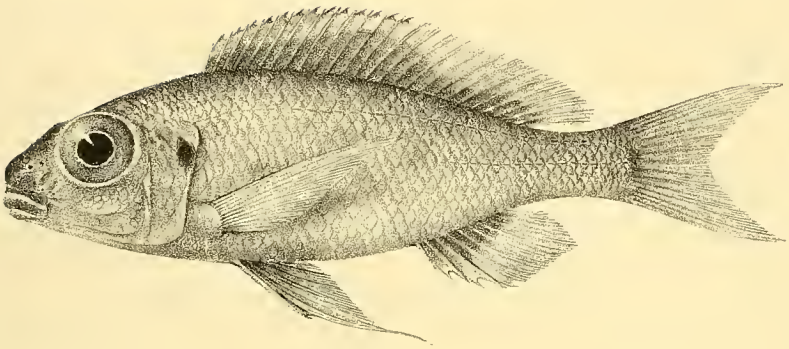
PLATE XIX.

PLATE XIX.

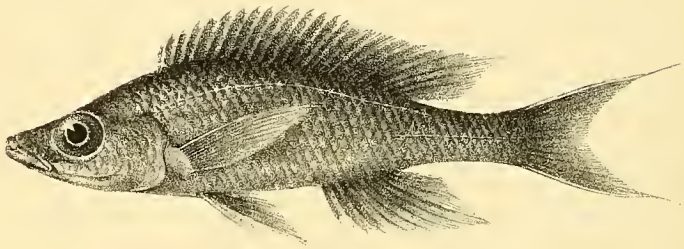
Fig. 1. *Paratilapia nigripinnis*, p. 152.
Fig. 2. „ *aurita*, p. 150.
Fig. 3. „ *calliura*, p. 151.
Fig. 4. *Ectodus longianalis*, p. 154.
Fig. 5. *Tilapia boops*, p. 158.
Fig. 6. „ *trematocephala*, p. 157.



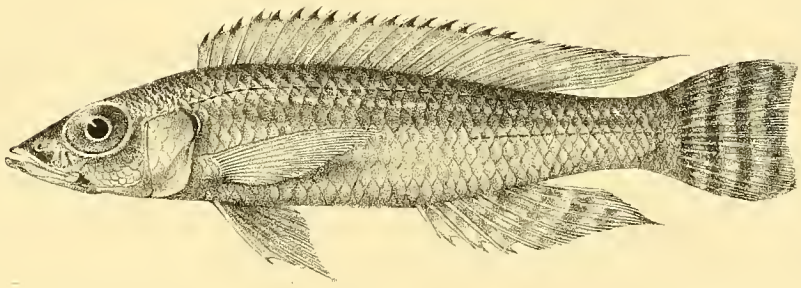
4.



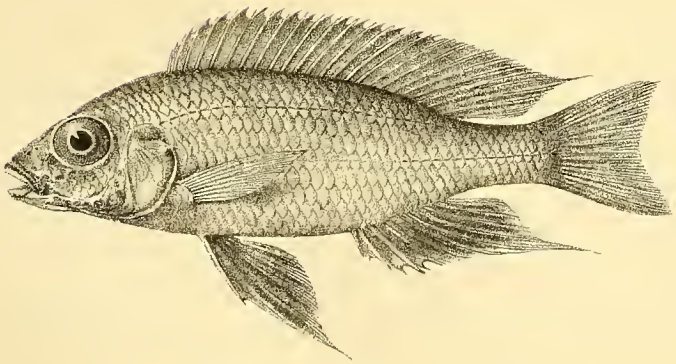
5.



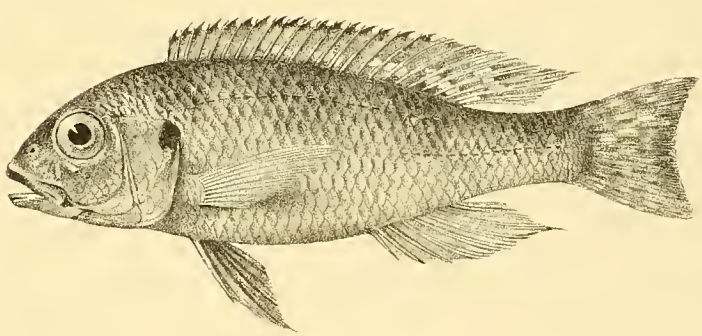
1.



3.



6.



2.

J Green del. et lith.

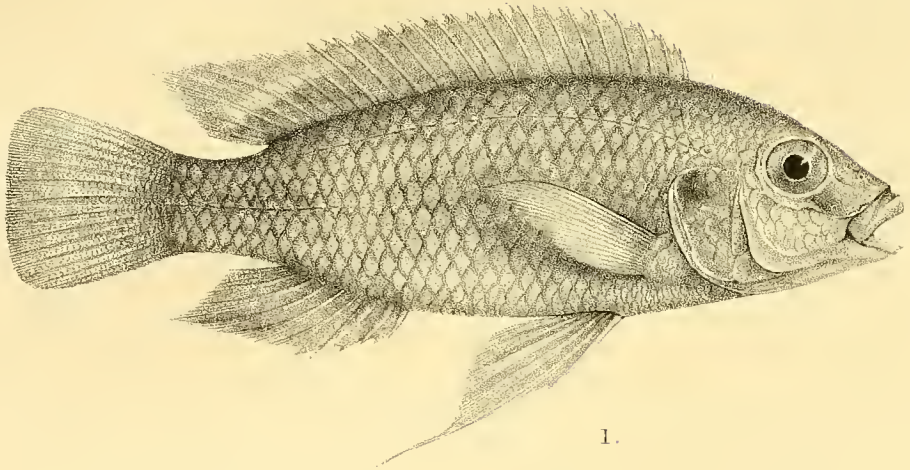
Mintern Bros. imp.

1. PARATILAPIA NIGRIPINNIS. 2. P. AURITA. 3. P. CALLIURA.
4. ECTODUS LONGIANALIS. 5. TILAPIA BOOPS. 6. T. TREMATOCEPHALA.

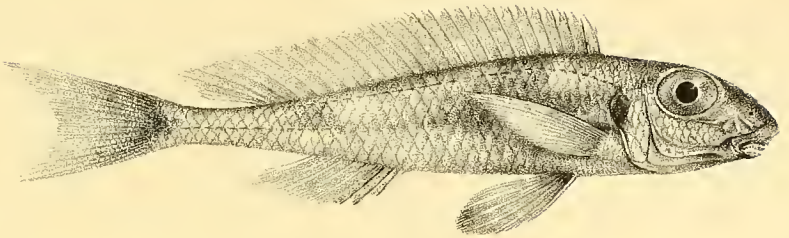
PLATE XX.

PLATE XX.

Fig. 1. *Gephyrochromis moorii*, p. 156.
Fig. 1 *a*. „ „ Open mouth. × 3.
Fig. 2. *Asprotilapia leptura*, p. 159.
Fig. 2 *a*. „ „ Lower view of head. × $1\frac{1}{2}$.
Fig. 2 *b*. „ „ Mouth. × 4.
Fig. 3. *Mastacembelus frenatus*, p. 159.
Fig. 4. „ *tæniatus*, p. 160.

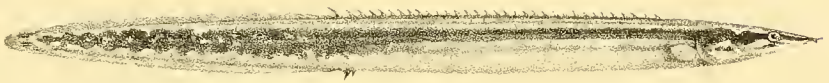


1.



2.

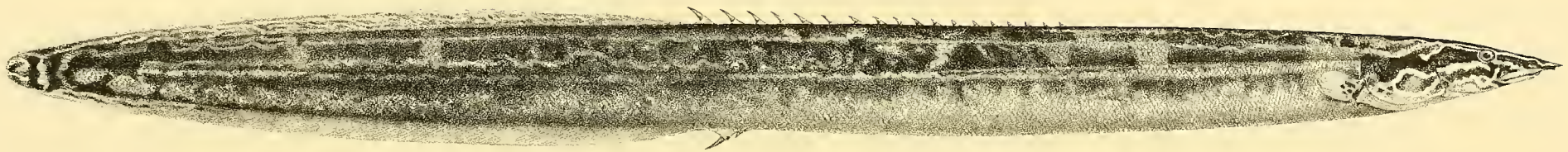
1a.



4.

2a.

2b.



3.

J. Green del. et lith.

Mintern Bros. imp.

1. GEPHYROCHROMIS MOORII. 2. ASPROTILAPIA LEPTURA.
3. MASTACEMBELUS FRENATUS. 4. M. TÆNIATUS.

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON
(continued).

		To Fellows. £	s.	d.	To the Public. £	s.	d.
VOLUME XIV. (1896–1898, containing 47 Plates) .	Price	5	5	0	7	0	0
Part 1. (1896, containing 2 Plates)	„	0	6	0	0	8	0
„ 2. (1896, containing 6 Plates)	„	0	9	0	0	12	0
„ 3. (1897, containing 9 Plates)	„	0	15	9	1	1	0
„ 4. (1897, containing 10 Plates)	„	1	10	0	2	0	0
„ 5. (1898, containing 2 Plates)	„	0	6	0	0	8	0
„ 6. (1898, containing 7 Plates)	„	0	18	0	1	4	0
„ 7. (1898, containing 6 Plates)	„	0	11	3	0	15	0
„ 8. (1898, containing 5 Plates and Title and Index)	„	0	9	0	0	12	0
VOLUME XV. (1898–1901, containing 52 Plates) .	Price	5	15	6	7	14	0
Part 1. (1898, containing 8 Plates)	„	0	15	9	1	1	0
„ 2. (1899, containing 5 Plates)	„	0	9	0	0	12	0
„ 3. (1899, containing 4 Plates)	„	0	9	0	0	12	0
„ 4. (1899, containing 4 Plates)	„	0	9	0	0	12	0
„ 5. (1900, containing 24 Plates)	„	2	12	6	3	10	0
„ 6. (1901, containing 4 Plates)	„	0	11	3	0	15	0
„ 7. (1901, containing 3 Plates and Title and Index)	„	0	9	0	0	12	0
VOLUME XVI.							
Part 1. (1901, containing 6 Plates)	Price	0	18	0	1	4	0
„ 2. (1901, containing 5 Plates)	„	0	11	3	0	15	0
„ 3. (1901, containing 9 Plates)	„	0	15	9	1	1	0

CONTENTS.

IV. *Third Contribution to the Ichthyology of Lake Tanganyika.—Report on the Collection of Fishes made by Mr. J. E. S. Moore in Lakes Tanganyika and Kivu during his Second Expedition*, 1899–1900. *By* G. A. Boulenger, *F.R.S.*, *F.Z.S.* (Plates XII.–XX.) . . . . . page 137

THE PUBLICATIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

The scientific publications of the Zoological Society of London are of two kinds—"Proceedings," published in an octavo form, and "Transactions," in quarto.

According to the present arrangements, the "Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the "Proceedings" by the Committee of Publication. A large number of coloured plates and engravings are attached to each annual volume of the "Proceedings," to illustrate the new or otherwise remarkable species of animals described in them. Among such illustrations, figures of the new or rare species acquired in a living state for the Society's Garden are often given.

The "Proceedings" for each year are issued in four parts, on the first of the months of June, August, October, and April, the part published in April completing the volume for the last half of the preceding year. Commencing from January 1901 they form two half-yearly volumes.

The "Transactions" contain such of the more important communications made to the scientific meetings of the Society as, on account of the nature of the plates required to illustrate them, are better adapted for publication in the quarto form. They are issued at irregular intervals.

Fellows and Corresponding Members, upon payment of a Subscription of £1 1*s.* before the day of the Anniversary Meeting in each year, are entitled to receive all the Society's Publications for the year. They are likewise entitled to purchase the Publications of the Society at 25 per cent. less than the price charged for them to the Public. A further reduction of 25 per cent. is made upon purchases of Publications issued prior to 1871, if they exceed the value of five pounds.

Fellows also have the privilege of subscribing to the Annual Volume of the 'Zoological Record' for a sum of £1 (which includes delivery in the United Kingdom *only*), but this privilege only holds good if the subscription is paid before the First of December in each year.

Such of these publications as are in stock may be obtained at the Society's Office (3 Hanover Square, W.), at Messrs. Longmans', the Society's publishers (Paternoster Row, E.C.), or through any bookseller.

October, 1901.

P. L. SCLATER,
Secretary.

TRANSACTIONS

OF

THE ZOOLOGICAL SOCIETY OF LONDON.

VOL. XVI.—PART 4.

LONDON:

PRINTED FOR THE SOCIETY,

SOLD AT THEIR HOUSE IN HANOVER-SQUARE;

AND BY MESSRS. LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

April 1902.

Price 12*s*.

Taylor and Francis, Printers,] [Red Lion Court, Fleet Street.

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

	To Fellows. £ s. d.	To the Public. £ s. d.
VOLUME I. (1833–1835, containing 59 Plates) . . Price	3 13 6	4 18 0*
VOLUME II. (1835–1841, containing 71 Plates) . . „	4 0 0	5 6 6*
VOLUME III. (1842-1849, containing 63 Plates) . . „	3 8 3	4 11 0*
VOLUME IV. (1851–1862, containing 77 Plates) . . „	6 2 0	8 2 6†
VOLUME V. (1862–1866, containing 67 Plates) . . „	5 4 3	6 19 0†
VOLUME VI. (1866–1869, containing 92 Plates) . . „	11 5 0	15 0 0†
VOLUME VII. (1869–1872, containing 73 Plates) . . „	10 4 0	13 12 0†
VOLUME VIII. (1872–1874, containing 82 Plates) . . „	9 8 3	12 11 0†
VOLUME IX. (1875–1877, containing 99 Plates) . . „	12 1 6	16 2 0†
VOLUME X. (1877–1879, containing 95 Plates) . . „	10 0 3	13 7 0†
GENERAL INDEX, Vols. I. to X. (1833–1879) . „	0 7 6	0 10 0
VOLUME XI. (1880–1885, containing 97 Plates) . . „	9 12 0	12 16 0
VOLUME XII. (1886–1890, containing 65 Plates) . . „	5 8 0	7 4 0
VOLUME XIII. (1891–1895, containing 62 Plates) . . „	6 8 3	8 11 0

* No copies of these volumes remain in stock.

† Only complete copies of these volumes are left in stock.

Continued on page 3 of Wrapper.

V. *On new or imperfectly-known Ostracoda, chiefly from a Collection in the Zoological Museum, Copenhagen.* *By* George Stewardson Brady, *M.D., LL.D., D.Sc., F.R.S., C.M.Z.S.*

Received February 11, read March 19, 1901.

[Plates XXI.–XXV.]

For the opportunity of examining and describing examples of most of the species noticed in this paper, I am indebted to the kindness of Drs. Meinert and H. J. Hansen, of the Zoological Museum at Copenhagen. The specimens were collected by different observers and in various parts of the world, the particulars as to collectors and habitat being recorded, so far as they are known to me, under the description of each species. As a supplement to this report, I have given in tabular form an account of the Ostracoda contained in a series of tow-net captures made in the North Atlantic by Dr. George Murray, F.R.S., of the Natural History Museum, South Kensington.

Among these there is a single new species—*Conchœcissa cucullata*—which I have to thank Dr. Murray for allowing me to describe here. This, indeed, is the only new species outside of the Copenhagen Collection which is noticed in the present paper.

Family ASTEROPIDÆ Brady & Norman.

Genus Asterope Philippi.

Asterope oculata, sp. nov. (Plate XXI. figs. 6–13.)

Shell of the *male* subovate: seen from the side (fig. 6) elliptical, slightly higher in front than behind, height equal to rather more than half the length; anterior extremity rounded, antennal notch rather wide and shallow; posterior extremity not so fully rounded and bearing two fascicles of hairs, one near the dorsal, the other near the ventral end; dorsal margin very feebly arched, often with a slight depression behind the middle, ventral somewhat more distinctly arched: seen from above (fig. 7) the outline is subcuneate, much wider in front than behind, the greatest width equal to about one-third of the length; anterior extremity obtusely pointed, almost mucronate; posterior subacute; lateral margins evenly curved, but flattened and almost rectilinear in the middle third. Surface of the shell smooth, whitish or cream-coloured, the large eyes showing very conspicuously as black circular patches beneath the middle of the dorsal margin. Length 1·35 mm.

The secondary branch of the antenna (fig. 10) is long and slender, and bears a strongly falcate terminal unguis, which towards its tapering extremity has a sigmoid twist, and at its base a single stout seta: in some cases, though not always, its outer margin is rather coarsely crenulated; the penultimate joint (dactylon) is elongated and bears three short setæ on the distal portion of its inner margin; the second joint of the mandibular foot (fig. 11) bears a short digitiform process in addition to the usual setæ, but there is no toothed process on the basal joint. Claws of the post-abdominal laminæ (fig. 12) five to eight, varying in number with the age of the specimen; margins devoid of spines or pectinations.

Female. Several of the terminal setæ of the antennules (fig. 9) are divided apically into lashes of fine filaments, and the concave margins of the postabdominal ungues (fig. 13) bear a few minute spines, the intervals between which are very finely pectinated. Shell shorter and broader than that of the male (fig. 8), greatest height situated behind the middle and equal to more than two-thirds of its length; anterior margin narrowly, posterior very broadly rounded; dorsal margin forming a flattened arch, ventral boldly arcuate. Eye-spot much smaller than in the male and paler in colour. Length 1 mm.

Hab. Taken in the surface-net at Trincomalee, Ceylon, plentifully; also at Cruz Bay. These gatherings consisted, with one or two exceptions, entirely of males.

Among a considerable number of specimens one female only could be found, and this occurred with only one or two males in the collection from Cruz Bay. I figure here in outline an example of both sexes from this locality. I think there can be little doubt as to its belonging to the female of this species, although there is a distinct pectinated armature of the postabdominal ungues which is not visible in the male. I have, however, already noticed [1] in a very closely allied species (*A. quadrata*) that the pectination of these ungues is more pronounced in the female than in the opposite sex. The Trincomalee specimens show a considerable diversity in the number of ungues, which, I think, may be accounted for by the differences of age.

ASTEROPE LICHENOIDES, sp. nov. (Plate XXIII. figs. 22–24.)

Shell of the *male* subquadrangular as seen from the side (fig. 22), about twice as long as broad; anterior extremity irregular, wide and obliquely truncated, the antennal notch forming a large and deep gap below the middle; posterior extremity rectangularly truncate, with a large rounded median prominence; dorsal margin gently convex, with a slight sinuation in front of the posterior angle, ventral very gently arcuate, with a slight posterior sinus: seen from above the outline is elongated, quadrate, wider in front than behind, all the angles very well marked, greatest width equal to half the length

[1] "On new or imperfectly known Species of Ostracoda, chiefly from New Zealand," Trans. Zool. Soc. London, vol. xiv. pt. viii. p. 432 (December 1898).

(fig. 23); anterior extremity wide, irregular, truncated, but with a very deep median sinus, posterior sharply truncated, but concave and fringed with hairs; lateral margins very irregular, with many sinuations, elevated at the anterior third whence they slope irregularly towards either extremity; surface of the shell marked throughout with extremely irregular crested ridges and bosses. Length 4·4 mm. Joints of the antennæ not produced into lateral spines, secondary branch with a narrow, elongated hand (fig. 24) which is slightly dilated distally and bears a brush of numerous hairs; terminal claw strongly falcate, bulbous at the base, and slightly so at the apex, a single stout seta at the base; penultimate joint of the mandibular foot bearing a digitiform appendage. Postabdominal laminæ armed with five long and slender pectinate claws.

Hab. Lat. 0° 37′ N., long. 109° 47′ E. One specimen only.

Genus Cyclasterope G. S. Brady [1].

This genus was founded on a species taken in Madras Harbour, the name being suggested by the circular outline of the shell, supplemented by certain anatomical characters. The shape of the shell can no longer be maintained as a generic character, several other species having been discovered, which with a very different form of shell combine the other distinctive characters of *Cyclasterope*. The points which I now suggest as diagnostic of the genus are the presence of a digitiform process on the penultimate joint of the mandibular foot, the profusely setiferous character of the vermiform limb, each ring of which toward the distal extremity usually supports two or three setæ, and the spinous armature of the joints of the swimming-branch of the antenna.

Cyclasterope fascigera, sp. nov. (Plate XXI. figs. 20–31.)

Male. Shell seen from the side subovate, slightly higher behind than in front, greatest height equal to rather more than half the length; left valve overlapping the right at the antero-dorsal angle, beneath which it is sinuated and forms a slightly prominent beak (fig. 20); anterior extremity of the right valve evenly rounded, the antennal notch deep and narrow; posterior extremity wider, rounded off, but strongly angulated in the middle and again between that point and the dorsum; dorsal margin almost flat for the greater part of its length, but gently curved behind, ventral forming a continuous gentle curve: seen from above the outline is elliptical (fig. 21), with broad, slightly rounded or subtruncate extremities; lateral margins gently and evenly arcuate, greatest width situated in the middle and equal to half the length. Surface of

[1] Trans. Zool. Soc. London, vol. xiv. pt. iii., 1897, p. 85: "A Supplementary Report on the Crustaceans of the Group Myodocopa, &c."

the shell smooth, fringed with rather long hairs on the anterior margin below the beak, slightly pubescent on the ventral aspect, the posterior extremity with a thick fringe of long hairs which ends abruptly both above and below. Colour yellowish-white. Length 6 mm. Sensory appendage of the antennule (fig. 24) large and very densely setiferous; joints of the swimming-branch of the antenna (fig. 25) spined on the outer margin—each spine as long as the following joint—and on the inner margin bearing fascicles of short hairs; secondary branch (fig. 26) having a long, flexuous claw which for the greater part of its length is more or less distinctly cross-furrowed and has a single stout seta near the base; basal joint bearing a few marginal hairs; second joint elongated, with sinuous margins and a brush of short setæ near the distal end (fig. 26); pectinated process of the mandibular foot rather feebly developed (fig. 27) and having seven or eight curved apical teeth; penultimate joint of the limb very densely setose; postabdominal laminæ of the usual type, each with 5 or 6 strongly pectinated ungues (fig. 29); spines of the larger ungues arranged in sequences, one large and one small alternately (fig. 30).

Female. Shell seen from the side broadly ovate, greatest height situated behind the middle and equal to nearly three-fourths of the length, the left valve overlapping the right posteriorly (fig. 22); anterior extremity narrowly rounded, beak and antennal notch well developed, posterior extremity distinctly angulated in the middle; dorsal and ventral margins very boldly arched, dorsal highest behind the middle, ventral quite evenly arcuate: seen from above (fig. 23) the outline is subovate, widest in the middle, about twice as long as broad; anterior extremity produced and subtruncate, posterior wider, rounded, the left valve produced much beyond the right; lateral margins arcuate, rather deeply sinuated behind the anterior extremity; surface of the shell smooth, with a few short hairs below the antennal notch. Length 5·2 mm. The "masticating" process of the mandibular foot (fig. 28) is more largely developed and more strongly serrated than in the male; the claws of the postabdominal laminæ are regularly spined (fig. 31), and the terminal joints of the mandibular foot are destitute of the setose covering which is found in the male.

Hab. Sourabaya (Java), several specimens, ♂ ♀; Chiribon (Java), 4½ fathoms, one specimen, ♂; Madeira, one specimen, ♂.

The fact of male and female specimens being found together in the same gathering leads to the supposition that both belong to the same species, though the remarkable differences in the shape of the shell may be thought to throw some doubt on that view of the matter. Pending further observation the two forms may be considered identical. The antennal setæ of this species are often much encumbered, or even glued together by crystalline calcareous concretions similar to those which I have already described and figured as occurring in *Philomedes sculpta*[1].

[1] "On new or imperfectly-known Ostracoda," *tom. cit.* p. 435.

Cyclasterope brevis (G. W. Müller). (Plate XXIV. figs. 16–22.)

Asterope brevis G. W. Müller, "Neue Cypridiniden," Zoologisch. Jahrbüch. vol. v. p. 239, pl. xxv. fig. 10, pl. xxvi. fig. 7, pl. xxvii. figs. 7–10, 15, 16.

Shell of the *female* seen from the side (fig. 16) almost circular, the length being only about one-seventh longer than the width, antennal notch situated slightly below the middle of the somewhat narrowed anterior extremity; posterior extremity boldly rounded, as is also the ventral margin; dorsal margin well arched, but flatter than the ventral; the right valve is slightly overlapped by the left throughout its entire circumference: seen from above the outline is elongated, ovate, nearly twice as long as broad, extremities obtusely rounded, rather narrower in front than behind. Shell-surface smooth; colour brown. Length 3·3 mm. The fifth joint of the antennule (fig. 17) has five marginal papilliform humps; the external margins of the antennal joints (fig. 18) are produced into very large, stout spines; the principal swimming-setæ are profusely ciliated and have, at intervals of five or six rings throughout the greater part of their length, delicate marginal spines (fig. 19); secondary branch of the antennæ (fig. 20) two-jointed, the first joint bearing five or six marginal hairs, the last a single long, ringed seta. Postabdominal laminæ armed with four finely pectinated claws (fig. 22).

Hab. St. Thomas, West Indies. Very few specimens, all females.

The male is unknown; the one female specimen described by Müller was taken off the coast of South America (Pernambuco): in all essential respects it seems to agree with those here noticed.

Cyclasterope similis, sp. nov. (Plate XXIII. figs. 25–29.)

Shell of the *female*, seen from the side, subelliptical, height equal to nearly two-thirds of the length (fig. 25); antennal notch rather wide and shallow, situated in the middle of the evenly rounded anterior extremity; posterior extremity as wide as the anterior, evenly rounded; dorsal margin almost rectilinear for the greater part of its length, ventral moderately arcuate; both extremities fringed with short hairs; surface smooth. Length 5 mm. Penultimate joint of the antennule (fig. 26) having a single large papilliform hump and a few fine marginal hairs: outer margins of the antennal joints, except the first, produced into long stout spines (fig. 27), first swimming-seta short and plumose, none of the setæ bearing marginal spines; secondary branch (fig. 28) indistinctly three-jointed, the last joint bearing a single ringed seta, the first five marginal hairs. Male unknown.

Hab. One specimen only, from a depth of 8 fathoms in Java Sound.

This species approaches *Asterope brevis* G. W. Müller in the single hump of the fifth antennular joint, but differs widely in the shape of the shell and the characters of the antennal swimming-setæ.

Family CYPRIDINIDÆ Baird.

Genus Cypridina M.-Edwards.

Cypridina granulosa, sp. nov. (Plate XXI. figs. 32–34.)

Shell of the *female*, seen from the side, elongated, subovate; height equal to two-thirds of the length (fig. 32); anterior extremity rounded, with a sharp downward-pointing beak; antennal notch near the middle line, rather wide and deep; posterior extremity narrowly rounded; dorsal margin evenly arched, highest in the middle, sloping steeply toward the posterior extremity; ventral margin gently arcuate: seen from above (fig. 33) the outline is narrowly ovate, twice as long as broad, greatest width in the middle. The shell is thin, membranous, and granular in appearance. Length 1·95 mm. Male unknown.

One specimen only. Memorandum of locality lost.

Cypridina foveolata, sp. nov. (Plate XXII. figs. 15–19.)

Shell of the *female*, seen from the side (fig. 15), elongated, ovate, produced behind into an obtuse median beak; greatest width situated in the middle and equal to two-thirds of the length; anterior extremity rounded, beak not prominent, antennal notch small and shallow; posterior extremity narrow, forming an obtuse subtriangular beak; dorsal and ventral margins boldly and evenly arched, the ventral the more arcuate of the two and forming a continuous curve throughout, the dorsal sinuated in front of the posterior beak: seen from above (fig. 16) the outline is ovate, widest in the middle, width equal to half the length, very narrowly rounded in front, subacuminate behind. Shell thin, smooth, almost membranous, marked throughout with small, closely-set circular impressions. Length 3·5 mm.

The soft parts present no abnormal characters; caudal laminæ (fig. 19) with four slightly curved, pectinated ungues.

Hab. China Sea. One specimen only.

Cypridina insolita, sp. nov. (Plate XXII. figs. 11–14.)

Shell of the *female* broadly ovate, tumid; seen from the side subovate, narrow in front, broadly and obliquely truncated behind, width equal to three-fourths of the length (fig. 11); anterior extremity narrow, rounded, beak short and sharp, antennal notch narrow and moderately deep; posterior extremity very irregularly sinuous; dorsal and ventral angles strongly marked, dorsal margin gently arcuate, ventral very boldly convex: seen from above (fig. 12) the outline is broadly ovate, widest in the middle, both extremities broadly rounded, width nearly equal to the height. Surface

of the shell marked with distant circular pittings, in the intervals of which are minute puncta. Length 3·7 mm. The antennal swimming-setæ, excepting the first, are densely plumose and without spines, the first much smaller, imperfectly jointed, non-plumose, and bearing several short but sharp marginal spines; secondary branch of the antenna simple, two-jointed, and bearing a long terminal seta (fig. 13). The vermiform limb has a simple terminal claw (fig. 14), beneath which is a large quadrate gap, and following this a still larger unjointed space beyond the ringed portion of the limb.

Hab. Java Sound, in a depth of 8 fathoms. One female only.

Genus Pyrocypris G. W. Müller.
(=*Eupathistoma* G. S. Brady.)

Pyrocypris americana G. W. Müller. (Plate XXI. figs. 14–19.)

Pyrocypris americana G. W. Müller, Neue Cypridiniden, *tom. cit.* p. 233, pl. xxv. fig. 3.

Shell, seen from the side, elongated, obliquely subquadrate, about twice as long as broad (fig. 14); anterior extremity narrow, beak short, obtusely pointed in front, acutely below, antennal notch small and narrow; posterior extremity produced into a prominent rounded beak; dorsal margin gently arcuate, sloping steeply behind, ventral boldly rounded in front, thence gently curved throughout its whole length; shell smooth, thin, chitinous. Length 2 mm. Secondary branch of the antenna (fig. 16) reduced to a fascicle of five short setæ; mandibular foot nearly as in *Cypridina* (fig. 17), bearing an ovate setiferous lobe and digitiform process; vermiform limb armed at the free extremity with three slender curved claw-like setæ (fig. 18), caudal laminæ (fig. 19) having four strong pectinated ungues and three shorter spine-like setæ. The first long seta of the antennule is dilated bulbously at the base (fig. 15), and bears a short tubular (?) barb (*a*) on the distal side of the bulb. The labial papillæ (phosphorescent organs of Müller) are not unlike those of *P. chierchiæ* (*Eupathistoma natans* Brady), which have been previously figured and described by me as sense-organs.

I do not fully understand the nature of the bulbous enlargement at the base of the antennular setæ, but it has an appearance somewhat similar to the poison-glands of the Cytheridæ, and I would suggest that it may have a similar function, the barb-like appendage being its efferent duct.

Taken by the 'Galathea' Expedition, Sept. 10th, 1875.

Specimens from this collection have been identified by Dr. G. W. Müller as belonging to *Pyrocypris americana*, which species was described from specimens taken off the west coast of Central America.

Pyrocypris chierchiæ G. W. Müller.

Pyrocypris chierchiæ G. W. Müller, *tom. cit.* p. 232, pl. xxv. figs. 1, 5, 6, pl. xxvi. figs. 12, 19, pl. xxvii. figs. 1, 2, 13, 14, 18, 24, 37.

Eupathistoma natans G. S. Brady, *tom. cit.* p. 437, pl. xliv. figs. 21–26.

Hab. Bay of Bengal: 'Galathea' Expedition, July 10th & 11th, 1896.

This and other species of *Pyrocypris* occur in immense numbers in tropical seas, and seem to contribute a very large share to the phosphorescence of those regions. This has been noticed by many authors. Dr. G. W. Müller notes that of *P. chierchiæ* as many as twenty thousand individuals were taken in a single haul, and of *P. revilli* fifteen thousand, and he attributes their light-producing faculty to the labial papillæ which, so far as at present appears, are peculiar to this genus.

Genus Philomedes Lilljeborg.

Philomedes sordida G. W. Müller. (Plate XXIV. figs. 23–26.)

Philomedes sordida G. W. Müller, *tom. cit.* p. 237, pl. xxv. fig. 17, pl. xxvi. fig. 17, pl. xxvii. figs. 28, 33.

Shell of the *male* (fig. 23), seen from the side, oblong-ovate, widest in the middle, scarcely twice as long as broad; anterior extremity narrow, rounded, without a beak, antennal notch forming a wide and shallow sinus quite on the ventral margin; posterior extremity broader, well rounded; dorsal margin well arched, forming an even curve throughout its entire length; ventral margin boldly arcuate from the antennal notch to the posterior extremity: margins of the valves fringed at both extremities with numerous closely-set setæ, which extend in front on to the ventral and behind on to the dorsal surface; right valve slightly overlapping the left in front: shell chitinous, its surface marked with small closely-set subrotund pittings. Length 1·55 mm.

The anatomy of the animal agrees generally with *Philomedes*, but the following characteristic points may be noted:—The secondary branch of the antenna (fig. 24) is extremely slender, the penultimate joint linear and bearing on its inner margin two short setæ, terminal joint dilated at the base, strongly curved and blunt, a long seta at the base and a short one near the extremity; vermiform limb bearing very few setæ, armed at the distal end with three small claws at one side of the gape and two on the other (fig. 25); postabdominal laminæ (fig. 26) with two large simple basally-pectinated terminal ungues, followed twice by sequences of a short and a long unguis, and finally three small setæ.

Hab. Cruz Bay. Three specimens, ♂. Müller's specimens were all females and were taken off the north of Japan.

Philomedes debilis, sp. nov. (Plate XXI. figs. 1–5.)

Shell of the *male*, seen from the side, ovate, widest in the middle, width equal to nearly two-thirds of the length (fig. 1); anterior extremity narrow, rounded, without a

beak, but with a shallow antennal notch just in front of the ventral margin, posterior margin broadly and evenly rounded; dorsal and ventral margins boldly and evenly arcuate: seen from above the outline (Pl. XXI. fig. 2) is regularly ovate, twice as long as broad, greatest width in the middle. Shell chitinous, smooth, its edges above and below the antennal notch bordered with a thin chitinous flange, within which is a nodulated crest having an appearance somewhat like the corneal lenses of an insect-eye (fig. 3). Length 1 mm. The antennæ are of the normal type, but with the first joint smaller than usual (fig. 4); caudal laminæ (fig. 5) narrow; at the proximal end three small ungues, followed by one larger, then three small and one larger, one small and two very much larger terminal claws.

Hab. Trincomali, Ceylon. Three specimens, ♂.

Genus Cypridinodes, gen. nov.

Like *Cypridina*, except as to the three pairs of maxillæ. The first pair (Pl. XXII. fig. 26) form a simple, elongated, triarticulate limb, which bears at its distal extremity several strongly pectinated claws and setæ; to the basal joint is attached a small single-jointed trisetose palp. The second maxilla (fig. 27) is in general build like that of *Philomedes* or *Cypridina*, but the principal masticating processes are armed with blunt nodular marginal teeth (fig. 27, *a–c*); third maxilla (fig. 28) without the hatchet-shaped lobe of *Cypridina*, which is replaced by a digitiform prolongation, retaining, however, something of the hatchet-shape.

Cypridinodes favus, sp. nov. (Plate XXII. figs. 20–31.)

Shell of the *female* seen from the side (fig. 20) broadly subovate, width equal to nearly three-fourths of the length; anterior extremity rectangularly truncated, posterior produced into a broad, truncated, subconical beak; dorsal and ventral margins boldly arched: seen from above (fig. 21) the outline is irregularly hexagonal, greatest width in the middle, and equal to two-thirds of the length; extremities wide and truncated, the anterior broadly mucronate, the posterior irregularly notched; lateral margins deeply furrowed in the middle, thence sloping steeply in a sinuous line to each extremity. Surface of the valves coarsely pitted with deep irregularly-angular impressions, and raised into two subcentral mammilliform elevations, between which is a deep transverse furrow; a little within, and parallel with, the ventral margins the central portion of the valve is bounded by an irregular jagged crest; the left valve is overlapped by the right in front and on the dorsal aspect. Length 3 mm. The penultimate joint of the antennule (fig. 22) has at its distal end a stout ringed seta, which bears a series of about twelve stout lash-like setæ arranged in a secund manner along its inner edge; two of the principal setæ of the terminal joint are dilated at their bases, forming a pair of globular or subglobular sacs; first seta of the swimming-

branch of the antenna (fig. 23) non-plumose, but bearing a series of about twelve lanceolate spines; secondary branch of the antenna three-jointed, with one terminal seta and one plumose seta on the first joint; mandibles as in *Cypridina*; caudal laminæ armed with six strong curved ungues, the first of which is strongly pectinated.

The locality of this species appears to have been lost.

Genus Codonocera, gen. nov. [1]

(? *Heterodesmus* Brady [2].)

Shell flat dorsally, very convex ventrally, with a well-marked anterior beak and antennal notch, and at the posterior extremity a wide rounded protuberance (Pl. XXII. fig. 1). The antennules bear at their apices, in addition to the ordinary sensory setæ, two shorter filaments (figs. 8, 9), which are dilated in the middle and divided distally into two branches, one of which is bifurcate, the other shorter and terminating in a bunch of six bell-shaped suctorial disks; secondary branch of the antenna (fig. 3) provided with a very large and powerfully muscular hand, the claw of which is marginally nodulated; mouth-organs as in *Philomedes*; postabdominal laminæ (fig. 7) with only three ungues.

Codonocera cruenta, sp. nov. (Plate XXII. figs. 1–10.)

Shell of the *male*, seen from the side (fig. 1), subquadrate, height equal to two-thirds of the length; anterior extremity rounded both above and below the notch; beak short and sharp; antennal notch moderately deep; posterior extremity wide, obliquely subtruncate, with a wide angular notch in the middle; dorsal margin straight, sloping steeply in front from its angulated extremity, rounded off posteriorly; ventral margin very boldly and evenly arcuate: seen from above (fig. 2) regularly ovate, widest in the middle, twice as long as broad; extremities subacuminate. Shell smooth, chitinous, pale-coloured, irregularly marked with black, stellate pigment-patches of various size, and with some pale clouded streaks near the centre of the valves. Length 2·8 mm. First swimming-seta of the antenna (fig. 3) short, non-plumose and spinous on the outer margin; secondary branch (fig. 3) very large, the hand armed with two strong spine-like setæ, which oppose the terminal claw; claw sigmoidally bent, nodulated on its inner edge and round the base of the outer edge; vermiform limb very sparingly setiferous, its apex armed with four small spines on the outer and one on the inner

[1] κώδων, a bell; κέρας, a horn.

[2] G. S. Brady: "On new or imperfectly-known Species of Marine Ostracoda," Trans. Zool. Soc. Lond. vol. v. p. 387.

side (fig. 6); copulatory organs large and massive (fig. 20), the vasa deferentia very distinct and wide. Postabdominal laminæ (fig. 7) short, with three very slightly curved, unequal, feebly pectinated claws. All the appendages of the animal are symmetrically blotched here and there with patches of red pigment.

Hab. Pulo Penang. One specimen, ♂.

The genus *Heterodesmus*, instituted many years ago for the reception of a single species taken in the China Sea, has in general form, though not in minor characters, a very marked resemblance to this species. It was described, however, from a single dried shell, from which the soft parts of the animal had almost entirely disappeared, so that it is impossible to say whether or no it might be properly referable to the genus here described.

Family SARSIELLIDÆ Brady & Norman.

Genus Sarsiella Norman.

Sarsiella (?) ornithoides, sp. nov. (Plate XXIII. figs. 16–21.)

Shell of the *female*, seen from the side, elongated, much produced both before and behind (fig. 16), fully twice as long as broad; anterior extremity produced into a subquadrate prominence which is about one-half the width of the valve and subtruncate or only slightly rounded in front, posterior forming a truncated conical protuberance; dorsal margin flattened, irregularly sinuated throughout; ventral margin boldly arcuate in the middle, sloping almost in a right line to the posterior extremity and forming a deep sinus beneath the anterior prominence; seen from above (fig. 17) elongated, subovate, more than twice as long as broad, with broadly mucronate prominences before and behind. Surface of the shell smooth, with a slight median longitudinal depression. Length 1 mm. Swimming-setæ of the antennæ very faintly plumose, but bearing fine marginal spines (fig. 19); secondary branch rudimentary, simple, digitiform, granulated (fig. 19). Postabdominal laminæ with two strong but almost straight toothless spines (fig. 21) and a few small setæ anteriorly.

Hab. Trincomalee, Ceylon. One specimen only.

The characters of the caudal laminæ seem to associate this species with *Sarsiella*, the shell also bearing some distant resemblance to that genus, but its position here must be regarded as purely provisional.

Family HALOCYPRIDÆ Claus.

Genus Conchœcia Dana.

Conchœcia spinirostris Claus.

Conchœcia spinirostris Claus, Die Halocypriden des atlantischen Oceans und Mittelmeeres, p. 56, pl. i. figs. 1–12.

A few specimens of both sexes from lat. 26° 15′ N., long. 29° 56′ W.; lat. 22° 20′ N., long. 27° 0′ W.; "*Patellaria* Syd overfladen" (Pacific), surface-net (females only).

Conchœcia striata Claus.

Conchœcia striata Claus, *loc. cit.* p. 62, pl. viii. figs. 1–6.

Taken in lat. 22° 55′ N., long. 29° 19′ W.

Genus Euconchœcia G. W. Müller.

Shell as in *Conchœcia*: groups of glands placed symmetrically at the postero-dorsal angles of the valves; frontal tentacle long, slender, and unjointed; antennule with three nearly equally long joints, the second of which is without setæ, while the third (coalescent third and fourth) instead of two sensory filaments bears a brush of about twenty setæ; last joint short, bearing one short and two long setæ, none of which are toothed. Secondary branch of the antenna with a slightly dilated basal joint, without papillary processes and with slender setæ; the three setæ of the last joint not of a sensory kind, but attached to the knee-like angle of the claw are two shorter setæ. Masticatory-plate of the mandible without setæ, the teeth numerous, short and stout. Last joint of the penultimate limb bearing setæ which are as long as the limb itself. Antennule of the female short, simple, two-jointed, bearing a terminal brush of setæ similar to that of the male.

This generic definition, so far as it applies to the male, is adapted from G. W. Müller (*loc. cit.*).

The only species is

Euconchœcia chierchiæ G. W. Müller. (Plate XXIV. figs. 9–15.)

Euconchœcia chierchiæ G. W. Müller, *loc. cit.* p. 277, pl. xxviii. figs. 1–10.

Shell, seen from the side, subquadrangular, elongated; twice as long as broad (fig. 9), produced in front into a prominent, curved beak, beneath which is a large sinus; posterior extremity subtruncate, rounded-off ventrally, and produced into a short spine (right valve only) dorsally; dorsal margin almost straight, or only slightly sinuated, ventral boldly arcuate. Length of the *male* 1·1 mm.; of the *female* ·85 mm.

The secondary branch of the antenna in the *female* (fig. 12) is two-jointed, the last joint short and bearing two long, but unequal setæ; that of the left side in the *male* is almost exactly similar, but on the right side bears as usual a very acutely angular hook-like claw (fig. 13). The ungues of the caudal lamina are five in number, very slender, and scarcely at all curved (fig. 15). The copulatory organ in the *male* is unusually broad and short (fig. 15).

Hab. The gathering here noticed consists of about equal numbers of males and females, and was taken at Cruz Bay. Müller's specimens, five in number and all males, were from the coast of Brazil.

Genus Conchœcissa Claus.

Conchœcissa cucullata, sp. nov. (Plate XXIV. figs. 1–8.)

Shell, seen from the side, oblong, much more than twice as long as broad; greatest width near the hinder extremity (fig. 1); anterior extremity forming a narrow, subcuneate, or hood-shaped prominence which is very acute at its apex, curvate on its ventral, and perfectly straight on its dorsal margin, a shallow notch on its posterior termination, from which point the ventral margin of the valve becomes boldly arcuate as far as the posterior extremity, which is well rounded below but obtusely rounded at the dorsal angle; dorsal margin almost perfectly straight, but armed behind with a few slender, backward-pointed spines; postero-dorsal angle of the left valve (figs. 1 & 2) produced into a very long spine-like process, below which is a broad curved sinus terminated by a short papilliform process, beyond which the curve of the ventral margin as far as the middle of its course is finely serrated; dorsal angle of the right valve rounded and spineless, but bearing a mammillated process like that of the opposite valve; there are groups of gland-cells connected with these processes and with the dorsal spine, and similar, but smaller, cells are continued for a considerable distance round the margin of the valves: seen from below the shell is elongated, subovate, widest in the middle, three times as long as broad, tapering nearly to the extremities, which are sharply mucronate. Surface of the valves sculptured with regular, subparallel wavy striæ, from which are given off numerous delicate cross striæ; the course of many of the larger striæ, especially on the posterior and ventral portions of the valves, being marked by small irregularly-placed circular pits or areolæ. The chewing-plates of the mandible (fig. 6) are armed with unusually short and blunt teeth, and are only sparingly setiferous. Antennule of the *female* (fig. 3) bearing five (or six?) equal terminal setæ, and one very short plumose hair; frontal tentacle very slender, linear, and sharply pointed, and having a sharp needle-like hair alongside of it; secondary branch of the antenna of the *female* (fig. 5) short, ovate, bearing two short, spine-like setæ and a brush of five sensory filaments of moderate and equal length, that of the

male (fig. 4) having four sensory setæ and a strongly falcate claw. Postabdominal laminæ armed with eight slender, curved, slightly pectinate claws, which increase progressively in length from before backward. The crop is excessively stout and muscular (fig. 8). Length 2·6 mm.

Hab. This appears to be a rather scarce species: the few specimens which were noticed occurred in plankton gatherings from the North Alantic, for the opportunity of examining which I am indebted to Dr. George Murray, F.R.S., of the Natural History Museum, South Kensington. The following are the localities:—Lat. 52° 27′·6 N., long. 15° 40′ W., 1570 fathoms (1 specimen); lat. 52° 18′·1 N., long. 15° 53′·9 W., 950 fathoms (1 specimen), 500 fathoms (1 specimen); lat. 52° 27′·6 N., long. 15° 40′ W., 1170 fathoms (1 specimen); lat. 52° 18′·1 N., long. 15° 53′·9 W., 1070 fathoms (3 specimens).

Only one male specimen was seen, and I failed to find the antennule, which had probably been detached in the process of capture.

The reference to the genus *Conchœcissa* must be taken as provisional only, as some important characters could not be clearly made out from the material at my command.

Family CYPRIDIDÆ.

Genus Cypris Müller.

Cypris virens (Jurine). (Plate XXIII. fig. 8.)

Several specimens collected by Dr. Meinert at Bona, Algiers, one of which is here figured, appear to be referable to *C. virens*, although differing somewhat from typical examples in the shorter and more tumid form of the shell. The soft parts conform accurately to the type.

Cypris flexilis, sp. nov. (Plate XXIII. figs. 11–15.)

Shell, seen from the side, oblong, subreniform, about twice as long as broad (fig. 11); anterior extremity moderately rounded, posterior rounded off above, obscurely angular below owing to a production of the left valve; dorsal margin forming a flattened arch, ventral very slightly sinuated in the middle. Shell extremely thin, flexible, and almost transparent. Length 4 mm. The swimming-setæ of the antennæ (fig. 12) reach scarcely to the apices of the terminal claws; principal ungues of the first pair of maxillæ finely ciliated, but without marginal spines; terminal claw of the first pair of feet (fig. 14) extremely long and slender, equal in length to the four preceding joints; caudal laminæ very long and slender, their posterior margins very finely (almost imperceptibly) ciliated; the terminal setæ, two apical and two marginal, crowded together at the distal extremity.

Hab. A few specimens taken at St. Croix, West Indies.

Cypris lætevirens, sp. nov. (Plate XXIII. figs. 3–5.)

Shell, seen from the side, elongated, subovate, highest in the middle; height slightly exceeding one-half of the length (fig. 3); extremities rounded, the anterior broad and rather flattened, the posterior narrower; dorsal margin evenly arcuate, highest in the middle where it is almost angular, ventral margin slightly sinuated in the middle: seen from above (fig. 4) ovate, twice as long as broad, widest in the middle; anterior extremity gently tapered and acuminate, posterior acuminate and more abruptly tapered; lateral margins evenly arcuate, slightly sinuated behind the anterior extremity. Surface of the shell smooth, finely hirsute, more particularly round the margins, thin, semitransparent. Colour very pale green. Length 2·55 mm. The swimming-setæ of the antennæ are plumose, and reach to the extremity of the limb; ungues of the first maxillæ destitute of marginal spines; postabdominal rami bearing four setæ (fig. 5), two at the apex, one of which is very short and delicate, the other quite half as long as the ramus itself; the two marginal setæ are rather closely approximated and of moderate size.

Hab. Puerto de St. Maria, near Cadiz.

Genus Cypridopsis Brady.

Cypridopsis aculeata Lilljeborg.

Numerous specimens taken at Puerto de St. Maria, near Cadiz.

Cypridopsis marmorata, sp. nov. (Plate XXIII. figs. 1, 2.)

Shell, seen from the side, subreniform (fig. 1), widest in the middle, scarcely twice as long as broad; extremities well rounded and nearly equal; dorsal margin boldly arched, ventral very slightly sinuated in the middle: seen from above (fig. 2) broadly ovate, widest behind the middle, width equal to two-thirds of the length, broadly rounded posteriorly, obtusely pointed in front. Surface of the valves covered with small, impressed puncta, and round the margins with fine, closely-set, short hairs; marked dorsally, after the manner of *C. vidua*, with three flexuous, transverse, deeply-coloured striæ. Length ·65 mm.

Hab. Bahia.

Subgenus Candonella Claus, Vávra [1].

Candonella virescens, sp. nov. (Plate XXV. figs. 16–29.)

Shell, seen from the side subreniform, highest in the middle, height equal to nearly two-thirds of the length (fig. 16); anterior extremity well rounded, posterior narrowly rounded-off below; dorsal margin very boldly arcuate, ventral distinctly sinuated in the

[1] Vávra, 'Die Süsswasser-Ostracoden Deutsch-Ost-Afrikas,' p. 12.

middle: seen from above elongate-ovate (fig. 17), more than twice as long as broad, lateral margins evenly arcuate, tapering to the extremities, of which the anterior is subacuminate, the posterior narrowly rounded. Surface of the shell smooth, pubescent, with very fine and rather closely-set short hairs (fig. 19); colour light green. The ventral margin of the left valve is produced in the centre so as to form an overlapping flange, which is marked by fine transverse striæ (fig. 18). Length ·87 mm. Swimming-setæ of the antennæ (fig. 6) reaching somewhat beyond the apices of the claws; terminal joint of the antennæ narrow, about one-third as long as the preceding joint: second pair of maxillæ (maxillipeds) in the female (fig. 22) digitiform, with a terminal brush of rather long setæ, and bearing an elongated palp which ends in one short and two very long setæ; in the *male* the limb is strongly prehensile, on the right side (fig. 24) thick, with angulated margins, and bearing a very broad, blunt, almost falcate terminal claw, on the left side (fig. 23) the limb is much narrower, is not marginally angulated, but has on the inner side a tuft of four or five small hairs and terminates in a sharply bent, hook-like claw; terminal unguis of the first pair of feet (fig. 25) stout and strongly curved; the second foot bears terminally two slender curved claws, one of which is very short, and a long seta; postabdominal rami (fig. 27) simple, cylindrical, each of them bearing a long terminal seta and another very minute seta placed a little on the proximal side of the apex. Copulative organs (fig. 28) elongated, very complex, ending in a somewhat hatchet-shaped intromittent process (?): on each side of the postabdominal rami in the *female* is situated an irregularly shaped laminar process —spermatheca? (fig. 29); the testes form two large ovoid coils of delicate spermatic tubes.

Hab. A gathering from Puerto de St. Maria, near Cadiz, contains numerous examples of this species.

The genus *Cypridopsis* proper is distinguished from the subgenus *Candonella* chiefly by a much greater tumidity of shell and by the armature and relative lengths of the last two joints of the antennæ—the penultimate joint in *Cypridopsis* being prolonged as far, or nearly as far, as the extremity of the last joint, and the claws being slightly different in the two sexes. Except as a matter of convenience, the differences seem to me scarcely sufficient to warrant the separation of *Candonella* as a subgenus.

Genus Cypretta Vávra[1].

Shell as in *Cypridopsis*. Second pair of legs forcipate. Postabdominal rami as in *Cypris*, but much smaller and more slender.

The name *Cypretta* has been applied by Vávra to this group as a subgenus of

[1] Vávra, "Süsswasser-Ostracoden Zanzibar's" (Jahrbuch der Hamburgischen wissenschaftlichen Anstalten xii. 1895).

Cypridopsis. The characters appear to me to be sufficiently distinct to warrant the adoption of the name as a generic one, and in any case the build of the caudal rami would seem to ally it more closely with *Cypris* than with *Cypridopsis*.

CYPRETTA SARSI, nom. nov. (Plate XXV. figs. 10–15.)

Cypridopsis minna G. O. Sars, Contributions to the Knowledge of the Freshwater Entomostraca of New Zealand, p. 30, pl. iv. figs. 3 *a–d*.

Shell extremely tumid, ovate; seen from the side ovoid, highest in the middle, height equal to two-thirds of the length (fig. 10), extremities well rounded, dorsal margin very boldly arcuate, ventral straight, with a slight median sinuation: seen from above (fig. 11) ovate, widest behind the middle, width equal to three-fourths of the length, broadly rounded behind, abruptly tapered and subacuminate in front; the right valve is higher and longer than the left, overlapping it a little dorsally and in front, also with a protuberant flange in the middle of the ventral margin (fig. 13); the anterior margin of the valves forms a narrow, produced lip, within and parallel with which is a series of 12–16 very conspicuous, curved, radiating black bands, connected at their extremities so as to mark off quadrangular spaces (fig. 12). Surface of the shell covered with minute circular impressions and fine hairs; on the dorsal aspect there is a conspicuous, sharply-defined, angular black patch (eye-spot) extending across the junction of the valves at their anterior third. Colour yellowish-brown; some of the larger specimens green. Length ·77 mm. Extremities of the second pair of legs produced into nodulated lip-like processes (fig. 14); postabdominal rami very slender, with two slender claws, the larger of which is nearly as long as the ramus. The body and limbs are marked with a few irregular red blotches.

Hab. St. Thomas, West Indies. Numerous specimens.

These specimens are I think, without doubt, identical with those described by Professor G. O. Sars under the name of *Cypridopsis minna* King. They do not, however, agree with those described by me [1] under that name, which are considerably higher in proportion to their length and have a glistening, yellowish, non-pubescent surface. Sars has, indeed, recognized the difference in outline, and supposes that both Mr. King's drawings and my own are probably incorrect owing to the difficulty of getting a nearly globular shell into accurate lateral or dorsal position; in this, however, he is mistaken, my drawings, and doubtless Mr. King's, being quite correct. Assuming my previous identification of the Australian specimens as *C. minna* King to be correct, it becomes necessary to give a new name to the present species. I have pleasure, therefore, in naming it after Professor G. O. Sars. And though Sars seems to agree with Mr. King in thinking that the varieties of colour—green, brown, and

[1] "Notes on Freshwater Entomostraca from South Australia," Proceedings of the Zoological Society of London, 1886, p. 91, pl. x. figs. 1–3.

yellow—noted by that author as occurring among his specimens may indicate distinct species, I am myself scarcely disposed to accept that view, for among the specimens here described there are many green ones, although the bulk are of the brownish colour so well described and figured by Professor Sars.

Genus Cyprinotus G. S. Brady.

Cyprinotus dentato-marginatus (Baird). (Plate XXIII. figs. 6, 7.)

Specimens apparently referable to this species were collected by Dr. Meinert at Bona, Algiers. I give a figure of one of these. It differs somewhat from Dr. Baird's figure, being rather more elongated, but has proportions similar to those figured by Prof. G. O. Sars in his paper on "Ostracoda and Copepoda raised from dried Australian mud." Dr. Baird's specimens were from Nagpur, India.

Cyprinotus fragilis, sp. nov. (Plate XXIII. figs. 9, 10; Plate XXV. figs. 37–39.)

Shell, seen from the side (Pl. XXV. fig. 37), very closely similar in outline to *C. prasina* Fischer, but entirely without surface-markings: seen from above (fig. 38) the posterior extremity is broader and more rounded, the anterior not so distinctly produced or sinuated; it is also wider in proportion to the length. Shell very thin and fragile, colourless. Length 1·5 mm.

I figure here some of the soft parts of the animal (Pl. XXIII. figs. 9, 10), which do not differ from those of the foregoing species.

Hab. Biskra, North Africa; females only (*Dr. Meinert*).

Genus Candonopsis Vávra [1].

Antennæ destitute of swimming-setæ. Mandibles and maxillæ with much elongated palps. Maxillipeds (second pair of maxillæ) with a rudimentary branchial plate bearing three or more plumose setæ. Posterior margins of the caudal rami without setæ.

Vávra's definition of this genus gives the "fan-plate" of the maxillipeds as bearing only three plumose setæ. None of the few specimens of *C. complanata* which I have dissected have had these limbs in a perfect condition, but the remains of at least five setæ were plainly visible in one of them. Inasmuch as in other respects the animals agree with the typical *Candonopsis*, it becomes necessary to modify the definition so far as regards the number of setæ.

Candonopsis complanata, sp. nov. (Plate XXV. figs. 30–36.)

Shell, seen from the side, elongated, subreniform, more than twice as long as broad (fig. 30), extremities rounded, equal, dorsal margin forming a flattened curve, almost

[1] Vávra, Monographie der Ostracoden Böhmens, 1891: Süsswasser-Ostracoden Zanzibar's, 1895.

straight in the middle and sloping steeply toward each extremity, ventral straight, with a slight median sinuation: seen from above (fig. 31) ovate, twice and a half as long as broad, acuminate in front, rounded behind, widest in the middle; left valve overlapping the right at both extremities. Surface of the shell smooth, whitish; anterior and posterior margins fringed with short hairs. Length 2 mm. The two principal ungues of the second maxillar segment laterally spined (fig. 32). Branchial plate of the maxillipeds (fig. 33) bearing five or six plumose setæ; last joint of the second foot (fig. 34) curved, with two small, but unequal hook-like apical claws, in front of which is a small adpressed marginal spine, one long apical seta and another of equal length arising from the middle of the joint; caudal rami with two slightly curved, pectinate, apical claws and two shorter setæ (fig. 35).

Hab. Biskra, North Africa (*Dr. Meinert*). Females only.

Family BAIRDIIDÆ Brady & Norman.

Genus Bairdia M'Coy.

Bairdia longisetosa, sp. nov. (Plate XXV. figs. 8, 9.)

Shell, seen from the side, elongated, subrhomboidal, height equal to more than half the length (fig. 8); anterior extremity broad, obliquely subtruncate, rounded off above and below, posterior produced to an acute submedian point; dorsal margin boldly arcuate, highest in the middle, thence sloping with a steep curve backward, more gently and with a distinct sinuation to the front; ventral margin nearly straight, rounded off in front, sloping upwards behind; the right valve is overlapped by the left everywhere, except at the upper part of the anterior extremity, and is much narrower and more sinuous in outline, its anterior margin slightly crenulated below, ventral margin armed posteriorly with a series of eight sharp backward-pointing spines; margins of the right valve devoid of spines: seen from above (fig. 9) the outline is regularly ovate, widest in the middle, acuminate behind, but wider in front, about twice as long as broad. Surface of the shell beset with hairs of moderate length, and, more especially toward the extremities, with extremely long and coarse hairs, some of them reaching one-third the length of the valves. Colour pale brown, semitransparent. Length 1·1 mm.

Hab. St. Thomas, West Indies. Four specimens.

Among known species, *Bairdia hirsuta* Brady is the one which bears most resemblance to the present, but the likeness is not remarkably close, except as to the setose clothing of the shell. *B. hirsuta* was taken by the 'Challenger' Expedition in 33°–38° South latitude in the Pacific at depths of from 1375–1825 fathoms. Both *B. hirsuta* and *B. villosa* are without marginal serrations or spines.

Family CYTHERIDÆ.

Genus Cythere Müller.

Cythere sicula, sp. nov. (Plate XXV. figs. 1–7.)

Shell of the *male* (fig. 1), seen from the side, elongated, subquadrangular, widest in front of the middle, more than twice as long as broad; anterior extremity broadly rounded, posterior obliquely subtruncate, rounded off at the angles; dorsal margin sloping steeply toward the front from the region of the hinge-tubercles, less steeply and with a gentle curve backward; ventral margin straight, with a slight sinuation anteriorly: seen from above (fig. 2) elongate-ovate, fully twice as long as broad, tapering evenly to the obtusely pointed extremities, greatest width in the middle. Right valve larger than the left, which it overlaps considerably on the dorsal and posterior margins; valve of the left side much narrower, with no elevation over the hinge-tubercle and distinctly excavated above the middle of its posterior margin. Valves fringed, except on the dorsal and middle of the ventral margins, with closely-set, short hairs; the marginal portions of the valves, more especially at the two extremities, form a smooth encircling flange which is marked radially by transverse lines prolonged from the bases of the fringing hairs; bordering the inner margin of the flange, the shell-surface is marked out into polygonal areas (fig. 4), the interspaces being dotted with small closely-set impressions; beneath the dorsal margin at its anterior third is, on each valve, a very conspicuous polished tubercle, partially surrounded by a smooth, non-punctate area. The shell of the *female* is nearly as long as that of the male, but wider, and the lower half of the posterior margin is prolonged into a wide angular beak (fig. 3). Length ·88 mm. The internal anatomy presents no characteristic features. The antennules, antennæ, and third pair of feet are here figured (figs. 5–7).

Hab. In fresh water, Syracuse. Numerous specimens of both sexes.

This species has many points of resemblance to *Cythere lutea* Müller and *C. rubida* Brady; but from the former it is separated by the more angular outline and the conspicuous marginal flange, from the latter by slight diversity of form as well as by its greater size and more delicate sculpture; both of these are, however, littoral marine forms, whereas the recorded habitat of *C. sicula* is "fresh water." One can easily imagine that differences such as characterise *C. sicula* may well have been produced by change of environment in species like *C. rubida* or *C. lutea*.

To Dr. George Murray, F.R.S., of the Natural History Museum, South Kensington, I am indebted for the opportunity of examining a series of Ostracoda from plankton collections made by him in the North Atlantic. The following list shows in tabular form the species found in each gathering, their comparative abundance or scarcity being noted roughly by the number of asterisks attached to each: * means scarcity; ** moderate number; *** abundance.

Locality.	Depth in fathoms.	*Conchœcia spinirostris* Claus.	" *magna* Claus.	" *maxima* Brady & Norman.	" *hyalophyllum* Claus.	" *porrecta* Claus.	" *striata* Claus.	*Paraconchœcia oblonga* Claus.	" *spinifera* Claus.	" *inermis* Claus.	" *gracilis* Claus.	*Conchœcilla lacerta* Brady & Norman.	*Conchœcissa imbricata* Brady.	" *cucullata*, sp. n.	*Microconchœcia clausii* G. O. Sars.	*Asterope* sp.
Lat. 52° 4′·5 N. Long. 12° 27′ W.	270	**	..	..	..	..	..	..	*							
	374	..	?													
	464	..	..	..	..	..	..	**								
	620	..	..	..	*	..	..	**	..	..	..	..	*			
	650	..	..	..	..	..	..	**								
Lat. 52° 18′·1 N. Long. 15° 53′·9 W.	Surface.	..	..	?												
	500	..	..	..	***	..	..	..	..	..	..	..	*			
	810	..	..	..	***	..	..	..	..	..	..	..	*			
	950	..	..	..	***	..	..	..	..	..	..	..	*			
	1070	**	***	..	..	..	..	..	..	..	**	*	*	*		
	1190	..	..	..	..	..	?	..	..	..	..	..	**			
	1300	..	..	..	..	..	***									
	1410	..	..	..	..	..	..	..	..	**	**	..	*	*	*	
	1510	**	..	..	***	..	..	..	..	..	..	..	**			
	1610	..	..	..	***	..	..	..	..	..	..	..	..	*	**	
	1710	..	..	..	..	***	..	..	..	..	..	..	**			
Lat. 52° 20′ N. Long. 15° 7′·9 W.	150	***	***													
	310 [1]															
	375	..	..	..	..	..	..	..	..	..	..	..	..	..	**	
	510	..	..	..	***	..	..	..	..	..	..	*	**			
	560	..	..	..	***	..	..	..	..	..	..	*	**			
Lat. 52° 27′·6 N. Long. 15° 40′ W.	790	..	..	..	..	..	..	..	?							
	920	..	..	*	..	..	..	..	..	..	..	..	*			
	1065	..	..	..	..	..	***									
	1170	..	..	**	..	..	..	..	..	..	..	..	..	*		
	1275	..	..	..	..	***	..	..	..	..	..	..	*	..	**	
	1370	..	*													
	1470	**	..	..	..	..	..	..	..	..	..	..	*			
	1570	..	**	..	..	..	..	..	..	..	..	..	*	*		
	1670	..	..	..	..	..	**	..	..	..	..	*	..	..	*	
	1770	..	..	*?												

[1] Many immature forms; species not recognizable.

PLATE XXI.

PLATE XXI.

Philomedes debilis, ♂ (p. 186).

Fig. 1. Outline of shell seen from right side, × 55.
2. ,, ,, above, × 55.
3. Margin of shell round antennal sinus, × 110.
4. Antenna seen from side, × 84.
5. One of the caudal laminæ, × 120.

Asterope oculata (p. 179).

Fig. 6. Shell of male seen from left side, × 40.
7. ,, ,, above, × 40.
8. Outline of shell of female seen from left side, × 40.
9. Antennule of female, × 100.
10. Internal branch of antenna of male, × 84.
11. Mandibular foot, × 100.
12. One of the caudal laminæ of male, × 84.
13. ,, ,, ungues of female, × 240.

Pyrocypris americana, ♀ (p. 185).

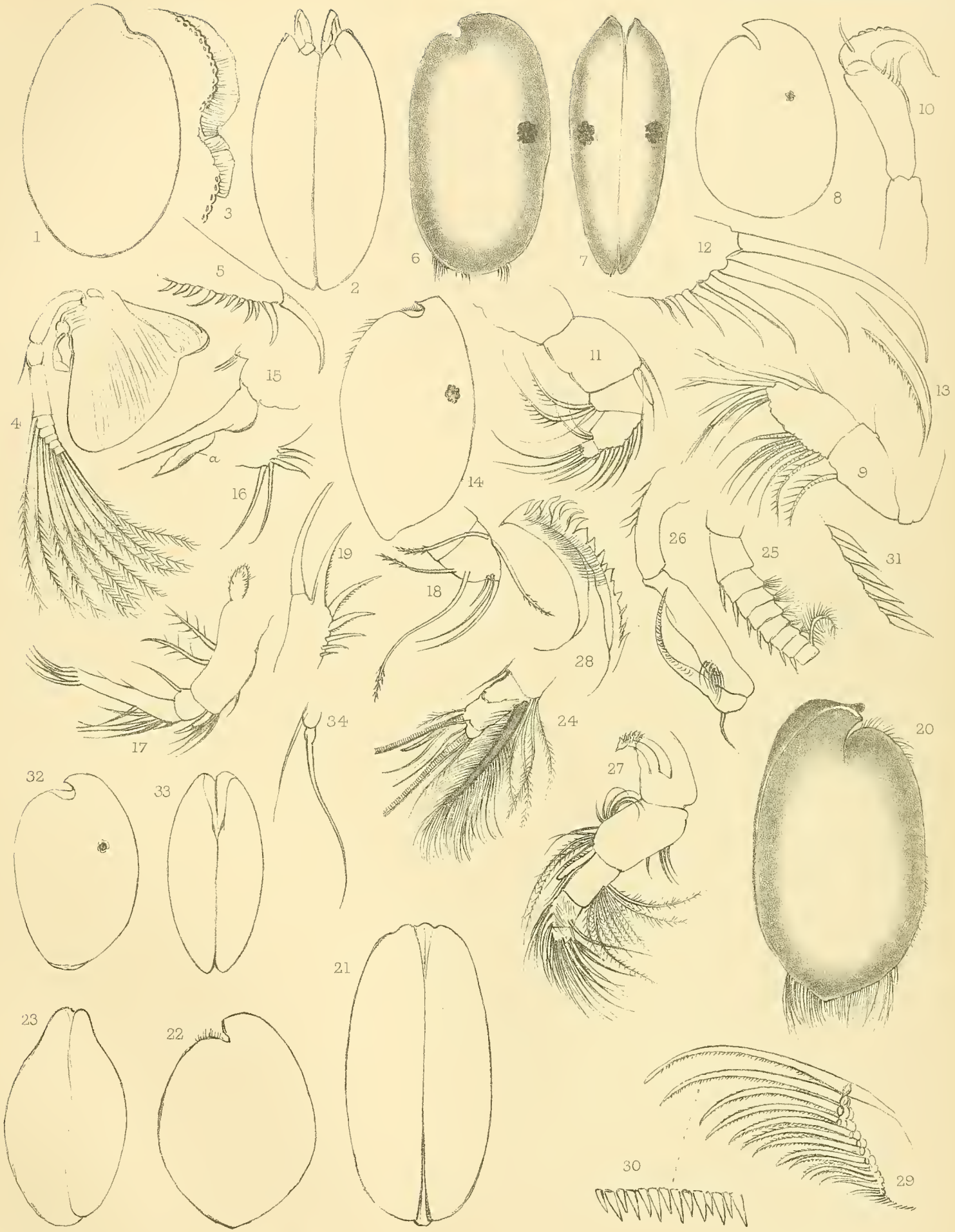
Fig. 14. Outline of shell, seen from left side, × 28.
15. Base of one of the principal antennular setæ, × 240.
16. Internal (rudimentary) branch of antenna, × 100.
17. Mandibular foot, × 84.
18. Apex of vermiform limb, with setæ, × 240.
19. Caudal lamina, × 100.

Cyclasterope fascigera (p. 181).

Fig. 20. Shell of male, seen from right side, × 10.
21. ,, ,, above, × 10.
22. Outline of shell of female, seen from left side, × 8.
23. ,, ,, ,, above, × 8.
24. Terminal joints and setæ of antennule of male, × 24.
25. Joints of antenna of male, × 40.
26. Internal branch of antenna of male, × 40.
27. Mandibular foot of male, × 26.
28. Masticating process of mandible of female, × 120.
29. Caudal laminæ of male, × 26.
30. Marginal armature of unguis of male, × 240.
31. ,, ,, ,, female, × 240.

Cypridina granulosa, ♀ (p. 184).

Fig. 32. Outline of shell of female, seen from left side, × 20.
33. ,, ,, ,, above, × 20.
34. Internal branch of antenna, × 150.



G.S.Brady, del.

Bale & Danielsson, Ltd, lith.

NEW OR IMPERFECTLY-KNOWN OSTRACODA.

PLATE XXII.

PLATE XXII.

Codonocera cruenta, ♂ (p. 188).

Fig. 1. Shell seen from left side, × 25.
2. „ „ above, × 25.
3. Antenna with internal (prehensile) branch and first swimming-seta (the other setæ omitted), × 84.
3 *a*. Armature of claw, × 240.
4. Mandibular foot, × 60.
5. Maxilla of second pair, × 115.
6. End of vermiform limb, with setæ, × 240.
7. Postabdominal laminæ, × 60.
8. Suctorial seta of antennule, × 200.
9. Suctorial discs of the same, × 440.
10. Copulatory organs.
(*v.d.*, vasa deferentia.)

Cypridina insolita, ♀ (p. 184).

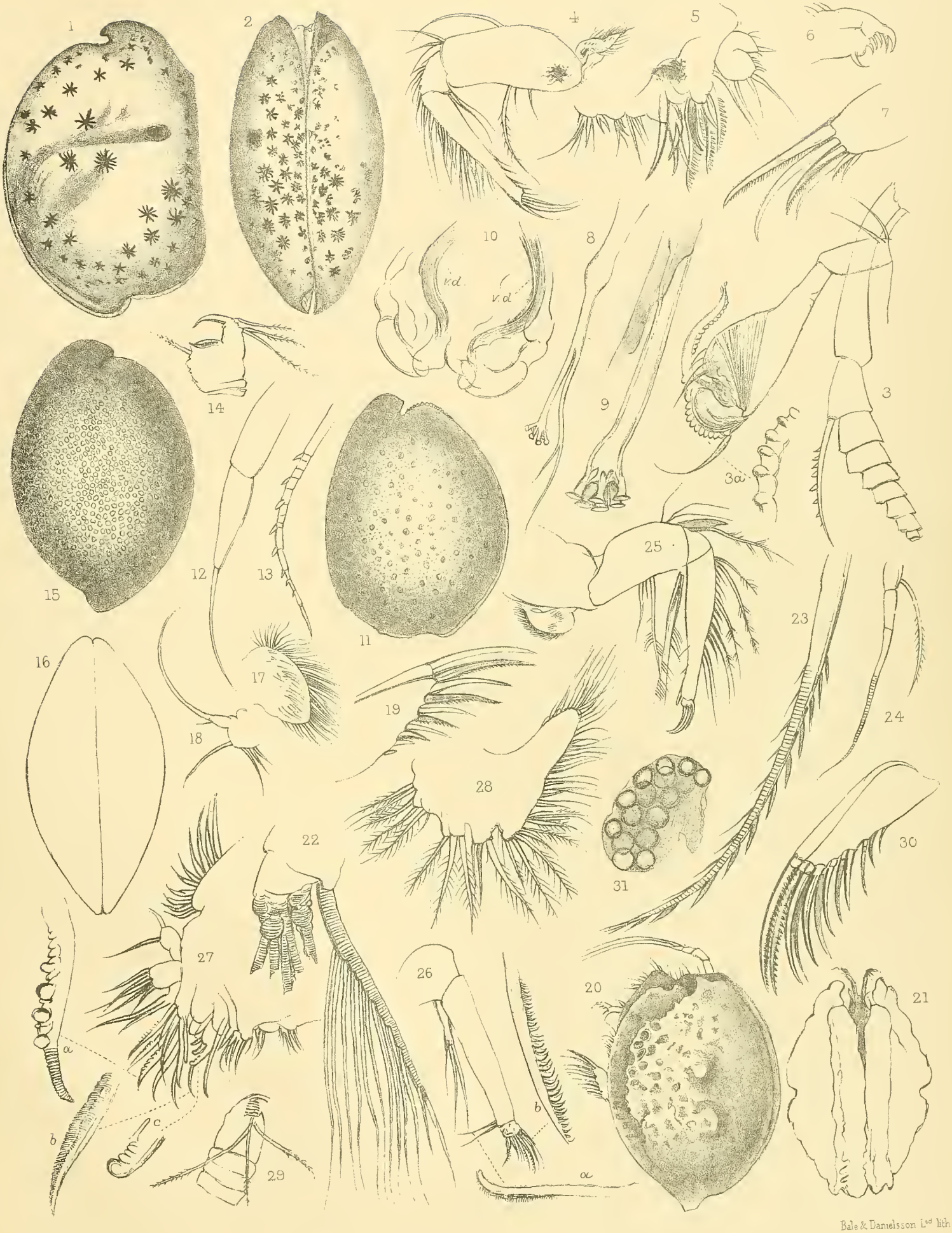
Fig. 11. Shell seen from right side, × 16.
12. Inner branch of antenna, × 115.
13. First swimming-seta of antenna, × 115.
14. End of vermiform limb, × 84.

Cypridina foveolata, ♀ (p. 184).

Fig. 15. Shell seen from right side, × 16.
16. „ „ above, × 16.
17. Process of mandibular foot, × 120.
18. End of vermiform limb, × 84.
19. Postabdominal laminæ, × 40.

Cypridinodes favus, ♀ (p. 187).

Fig. 20. Shell seen from left side, × 16.
21. „ „ above, × 16.
22. Last two joints and setæ of antennule, × 300.
23. One of the swimming-setæ of antenna, × 240.
24. Inner branch of antenna, × 115.
25. Mandibular foot, × 55.
26. Maxilla of first pair, × 55.
26 *a*, *b*. Setæ of the same, × 300.
27. Maxilla of second pair, × 84.
27 *a*, *b*, *c*. Setæ of the same, × 300.
28. Maxilla of third pair, × 84.
29. End of vermiform limb, × 120.
30. Postabdominal laminæ, × 55.
31. Eye, × 84.



Bale & Danielsson Ltd lith

G.S.Brady. del.

NEW OR IMPERFECTLY-KNOWN OSTRACODA.

PLATE XXIII.

PLATE XXIII.

Cypridopsis marmorata (p. 193).

Fig. 1. Shell, seen from right side, × 84.
2. „ „ above, × 84.

Cypris lætevirens (p. 193).

Fig. 3. Shell, seen from left side, × 25.
4. „ „ above, × 25.
5. Postabdominal ramus, × 84.

Cyprinotus dentato-marginatus (p. 196).

Fig. 6. Shell, seen from left side, × 40.
7. Anterior margin of the right valve, × 84.

Cypris virens (p. 192).

Fig. 8. Shell, seen from left side, × 16.

Cyprinotus fragilis (p. 196).

Fig. 9. End of second foot, × 240.
10. Postabdominal ramus, × 90.

Cypris flexilis (p. 192).

Fig. 11. Outline of shell, seen from right side, × 16.
12. Antenna, × 40.
13. Maxilliped, × 40.
14. Foot of first pair, × 40.
15. Postabdominal ramus, × 40.

Sarsiella ornithoides (p. 189).

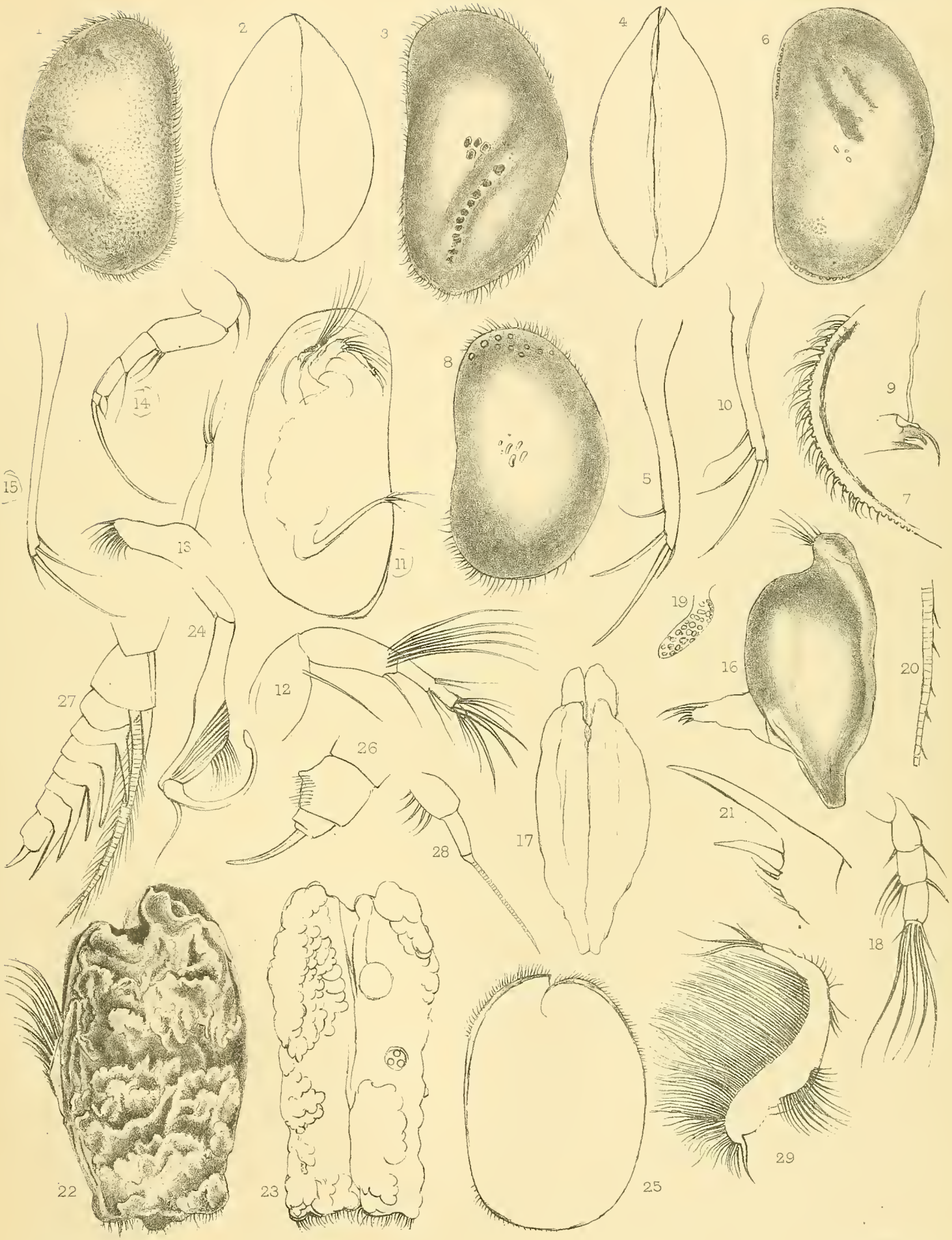
Fig. 16. Shell, seen from left side, × 55.
17. „ „ above, × 55.
18. Antennule (imperfect), × 60.
19. Inner branch of antenna, × 320.
20. Portion of one of the antennal setæ, × 320.
21. Postabdominal lamina, × 240.

Asterope lichenoides, ♂ (p. 180).

Fig. 22. Shell, seen from left side, × 16.
23. „ „ above, × 16.
24. Inner branch of antenna, × 50.

Cyclasterope similis, ♀ (p. 183).

Fig. 25. Outline of shell, seen from right side, × 12.
26. Last two joints of antennule, × 55.
27. Joints and first seta of antenna, × 55.
28. Inner branch of antenna, × 84.
29. Maxilla of first pair, × 40.



G.S.Brady. del.t

Bale & Danielsson, Ltd. lith

NEW OR IMPERFECTLY-KNOWN OSTRACODA.

PLATE XXIV.

PLATE XXIV.

Conchœcissa cucullata (p. 191).

Fig. 1. Shell (with open valves) seen from outside, × 40.
2. Shell seen from left side, × 40.
3. Antennule (with frontal tentacle) of female, × 84.
4. Inner branch of antenna of male, × 84.
5. „ „ female, × 84.
6. Chewing-plates of mandible, × 240.
7. Postabdominal lamina, × 84.
8. Gullet and stomach, × 84.

Euconchœcia chierchiæ (p. 190).

Fig. 9. Outline of shell, ♂, seen from left side, × 55.
10. Antennule of male, × 120.
11. „ female, × 120.
12. Antenna of female, × 110.
13. Inner branch of antenna of male, × 110.
14. Mandible and palp of female, × 120.
15. Copulatory organ and caudal laminæ of male, × 110.

Cyclasterope brevis, ♀ (p. 183).

Fig. 16. Outline of shell seen from right side, × 16.
17. Last three joints of antennule (setæ omitted), × 55.
18. Joints and first seta of antenna, × 84.
19. Portion of one of the antennal setæ, × 240.
20. Inner branch of antenna, × 84.
21. Maxilla of first pair, × 40.
22. Postabdominal laminæ, × 40.

Philomedes sordida, ♂ (p. 186).

Fig. 23. Outline of shell seen from left side, × 40.
24. Inner branch of antenna, × 100.
25. End of vermiform limb, with setæ, × 240.
26. One of the caudal laminæ, × 100.

G.S.Brady, del.ᵗ

Bale & Danielsson, Ltd. lith.

NEW OR IMPERFECTLY-KNOWN OSTRACODA.

PLATE XXV.

PLATE XXV.

Cythere sicula (p. 198).

Fig. 1. Shell of male, seen from left side, × 45.
2. ,, ,, above, × 45.
3. Shell of female, seen from left side, × 45.
4. Portion of anterior margin of shell, × 240.
5. Antennule of male, × 120.
6. Antenna of male, × 120.
7. Foot of third pair, × 100.

Bairdia longisetosa (p. 197).

Fig. 8. Shell, seen from right side, × 35.
9. ,, ,, above, × 35.

Cypretta sarsi (p. 195).

Fig. 10. Shell, seen from left side, × 50.
11. ,, ,, above, × 50.
12. Portion of anterior margin of shell, × 84.
13. Ventral margin of right valve, seen from inside, × 84.
14. Terminal joint of last foot, × 440.
15. Postabdominal ramus, × 240.

Candonella virescens (p. 193).

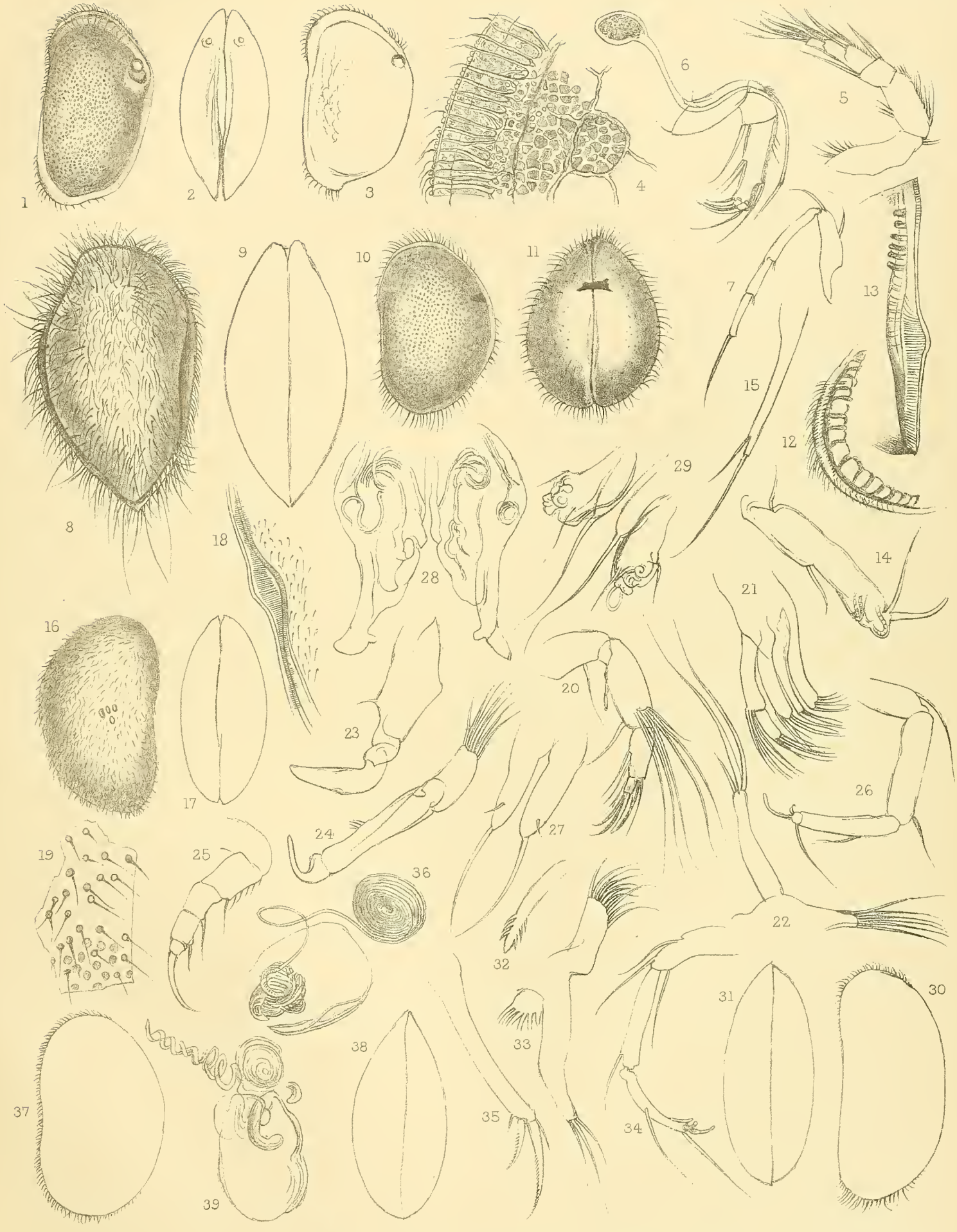
Fig. 16. Shell, seen from right side, × 46.
17. ,, ,, above, × 46.
18. Ventral margin of left valve, seen from inside, × 84.
19. Portion of shell, × 240.
20. Antenna, × 120.
21. Maxilla, × 240.
22. Maxilliped of female, × 240.
23. ,, male, left side, × 240.
24. ,, ,, right side, × 240.
25. Foot of first pair, × 120.
26. ,, last pair, × 240.
27. Caudal rami, × 240.
28. Copulatory organ of male, × 240.
29. Spermatheca and caudal rami of female, × 240.

Candonopsis complanata (p. 196).

Fig. 30. Outline of shell, seen from left side, × 25.
31. ,, ,, above, × 25.
32. Spine of second digit of maxilla, × 120.
33. Maxilliped of female with basal portion of palp, × 120.
34. Leg of second pair, × 84.
35. Caudal ramus, × 84.
36. Spermatheca of female, with spermatic coil, × 120.

Cyprinotus fragilis, ♀ (p. 196).

Fig. 37. Outline of shell, seen from left side, × 25.
38. ,, ,, above, × 25.
39. Spermatheca with spermatic coil, × 120.



G.S.Brady, del.ᵗ

Bale & Danielsson, Lᵗᵈ, lith.

NEW OR IMPERFECTLY-KNOWN OSTRACODA

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON
(*continued*).

	To Fellows. £ s. d.	To the Public. £ s. d.
VOLUME XIV. (1896–1898, containing 47 Plates) .	Price 5 5 0	7 0 0
Part 1. (1896, containing 2 Plates)	„ 0 6 0	0 8 0
„ 2. (1896, containing 6 Plates)	„ 0 9 0	0 12 0
„ 3. (1897, containing 9 Plates)	„ 0 15 9	1 1 0
„ 4. (1897, containing 10 Plates)	„ 1 10 0	2 0 0
„ 5. (1898, containing 2 Plates)	„ 0 6 0	0 8 0
„ 6. (1898, containing 7 Plates)	„ 0 18 0	1 4 0
„ 7. (1898, containing 6 Plates)	„ 0 11 3	0 15 0
„ 8. (1898, containing 5 Plates and Title and Index)	„ 0 9 0	0 12 0
VOLUME XV. (1898–1901, containing 52 Plates) .	Price 5 15 6	7 14 0
Part 1. (1898, containing 8 Plates)	„ 0 15 9	1 1 0
„ 2. (1899, containing 5 Plates)	„ 0 9 0	0 12 0
„ 3. (1899, containing 4 Plates)	„ 0 9 0	0 12 0
„ 4. (1899, containing 4 Plates)	„ 0 9 0	0 12 0
„ 5. (1900, containing 24 Plates)	„ 2 12 6	3 10 0
„ 6. (1901, containing 4 Plates)	„ 0 11 3	0 15 0
„ 7. (1901, containing 3 Plates and Title and Index)	„ 0 9 0	0 12 0
VOLUME XVI.		
Part 1. (1901, containing 6 Plates)	Price 0 18 0	1 4 0
„ 2. (1901, containing 5 Plates)	„ 0 11 3	0 15 0
„ 3. (1901, containing 9 Plates)	„ 0 15 9	1 1 0
„ 4. (1902, containing 5 Plates)	„ 0 9 0	0 12 0

CONTENTS.

V. *On new or imperfectly-known Ostracoda, chiefly from a Collection in the Zoological Museum, Copenhagen.* *By* George Stewardson Brady, *M.D., LL.D., D.Sc., F.R.S., C.M.Z.S.* (Plates XXI.–XXV.) . . . . . page 179

THE PUBLICATIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

The scientific publications of the Zoological Society of London are of two kinds—"Proceedings," published in an octavo form, and "Transactions," in quarto.

According to the present arrangements, the "Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the "Proceedings" by the Committee of Publication. A large number of coloured plates and engravings are attached to each annual volume of the "Proceedings," to illustrate the new or otherwise remarkable species of animals described in them. Among such illustrations, figures of the new or rare species acquired in a living state for the Society's Gardens are often given.

The "Proceedings" for each year are issued in four parts, on the first of the months of June, August, October, and April, the part published in April completing the volume for the last half of the preceding year. Commencing from January 1901 they form two half-yearly volumes.

The "Transactions" contain such of the more important communications made to the scientific meetings of the Society as, on account of the nature of the plates required to illustrate them, are better adapted for publication in the quarto form. They are issued at irregular intervals.

Fellows and Corresponding Members, upon payment of a Subscription of £1 1*s.* before the day of the Anniversary Meeting in each year, are entitled to receive all the Society's Publications for the year. They are likewise entitled to purchase the Publications of the Society at 25 per cent. less than the price charged for them to the Public. A further reduction of 25 per cent. is made upon purchases of Publications issued prior to 1871, if they exceed the value of five pounds.

Fellows also have the privilege of subscribing to the Annual Volume of the 'Zoological Record' for a sum of £1 (which includes delivery in the United Kingdom *only*), but this privilege only holds good if the subscription is paid before the First of December in each year.

Such of these publications as are in stock may be obtained at the Society's Office (3 Hanover Square, W.), at Messrs. Longmans', the Society's publishers (Paternoster Row, E.C.), or through any bookseller.

April, 1902.

P. L. SCLATER,
Secretary.

TRANSACTIONS

OF

THE ZOOLOGICAL SOCIETY OF LONDON.

VOL. XVI.—PART 5.

LONDON:

PRINTED FOR THE SOCIETY,

SOLD AT THEIR HOUSE IN HANOVER-SQUARE;

AND BY MESSRS. LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

October 1902.

Price 18*s*.

Taylor and Francis, Printers,] [Red Lion Court, Fleet Street.

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

	To Fellows. £	s.	d.	To the Public. £	s.	d.
VOLUME I. (1833–1835, containing 59 Plates) . . Price	3	13	6	4	18	0*
VOLUME II. (1835–1841, containing 71 Plates) . . „	4	0	0	5	6	6*
VOLUME III. (1842–1849, containing 63 Plates) . . „	3	8	3	4	11	0*
VOLUME IV. (1851–1862, containing 77 Plates) . . „	6	2	0	8	2	6†
VOLUME V. (1862–1866, containing 67 Plates) . . „	5	4	3	6	19	0†
VOLUME VI. (1866–1869, containing 92 Plates) . . „	11	5	0	15	0	0†
VOLUME VII. (1869–1872, containing 73 Plates) . . „	10	4	0	13	12	0†
VOLUME VIII. (1872–1874, containing 82 Plates) . . „	9	8	3	12	11	0†
VOLUME IX. (1875–1877, containing 99 Plates) . . „	12	1	6	16	2	0†
VOLUME X. (1877–1879, containing 95 Plates) . . „	10	0	3	13	7	0†
GENERAL INDEX, Vols. I. to X. (1833–1879) . „	0	7	6	0	10	0
VOLUME XI. (1880–1885, containing 97 Plates) . . „	9	12	0	12	16	0
VOLUME XII. (1886–1890, containing 65 Plates) . . „	5	8	0	7	4	0
VOLUME XIII. (1891–1895, containing 62 Plates) . . „	6	8	3	8	11	0

* No copies of these volumes remain in stock.

† Only complete copies of these volumes are left in stock.

Continued on page 3 of Wrapper.

VI. *On the Myology of the Tongue of Parrots, with a Classification of the Order, based upon the Structure of the Tongue.* *By* Geo. P. Mudge, *A.R.C.S. Lond., F.Z.S., Lecturer on Biology, London School of Medicine for Women; and Demonstrator of Biology, London Hospital Medical School.*

Received March 4, read April 2, 1901.

[Plates XXVI.–XXIX. & Text-figures 1–16.]

This investigation owed its origin to a suggestion of Prof. Howes, and was commenced in 1896, during my tenure of the Marshall Scholarship, in the Huxley Laboratory, Royal College of Science, London. A preliminary paper was communicated to this Society in 1897, but its subject matter was not published, as it was deemed advisable to incorporate it in the finished work.

I have to express my thanks to the Prosector of the Society, to Professors Stewart, Howes, and D'Arcy Thomson, and to Mr. W. P. Pycraft, for the loan of the greater portion of my material. To my past teacher, Professor Howes, and to Dr. P. Chalmers Mitchell I have further to express my thanks for valuable advice given in the preparation of the manuscript for the press.

The scientific names of the Parrots, the tongues of which I have described, are those adopted by Salvadori. With but a few exceptions, the birds have been very carefully compared with his descriptions, as made in his Catalogue of Parrots, and in those cases (when tongues only were supplied to me) where identification was not possible, I have carefully worked out the synonymy.

With regard to technical terms, I follow the osteological terms of Mivart (6 & 7) and the myological of Gadow (4) and of Nitzsch (2).

The classification of the Order, appended to this memoir, is designed merely as an index showing the general trend of the ascertained facts relating to the tongue.

Part I.—HISTORICAL.

Although the Parrots have occupied the attention of naturalists to a considerable extent, their tongues, so far as internal structure is concerned, have received but little notice.

It is now nearly forty years since Giebel described the hyoid bones of several species of Parrots, and more than thirty since Nitzsch's paper was published in which the lingual myology of *Ara macao* (*Psittacus macao* Nitzsch) and *Chrysotis leucocephala*

(*Psittacus leucocephala* Nitzsch) was described, and I have been unable to find any record either before or since this paper which deals with the subject.

The reason of this neglect is not far to seek, for I suppose that the tongue is about the last structure in which the zoologist would seek for characters indicative of affinity. But yet its characters, as affording a basis for classification, have not been altogether neglected, for Baird, in his 'Review of North-American Birds,' has founded a genus, *Perissoglossa*, upon them, and Gadow, in his paper "On the Structure of certain Birds from Hawaii," has laid stress on the shape and structure of the tongue. How little such characters are to be relied upon at present is indicated by the diverse results they have obtained, for the one would ally the Cœrebidæ to the Sylvicolidæ, and the other to the Drepanididæ.

Further, Lucas, in the 'Auk' for 1894, has shown that the characters of the tongue of birds have neither morphological nor physiological significance, "for while the skulls of two genera are widely separated their tongues are structurally alike," and "while certain birds (*Certhiola*) may possess a tongue adapted for honey-sucking, they may yet possess a distinct liking for insects." He has also shown that the "Sandwich Islands Drepanididæ have a perfect tubular tongue, and some of the Meliphagidæ have a suctorial apparatus and could thus feed on honey and nectar if they chose. Some of them, as their stomachs testify, feed on fruit, some on spiders and insects."

In the midst of such negative results came Mivart's paper (6) on the "Hyoid Bone of Parrots," in which he demonstrated that this structure did possess characters of classificatory value and by means of which the Loriidæ were marked off as a group distinct from the Psittacidæ. Working at the myology, I have not only corroborated Mivart's conclusion, but also that of Beddard and Parsons which was based upon a study of the patagial tendons and the bronchial rings, and have further arrived at results which, as I trust to show in the course of this paper, justify us in using the characters of the tongue for purposes of classification.

With respect to the literature, the earliest paper on the subject is by von Giebel (1), who in 1858 described and figured the hyoid bones of several species of Parrots which were then included under the genus *Psittacus*. In 1862 Nitzsch published a paper entitled "Zur Anatomie der Papageien" (2), in which the myology of the tongue of "*Psittacus*" [1] was described for the first time.

The next paper appeared after a considerable interval, and it was only in 1886 that Shufeldt, dealing with the osteology of *Conurus carolinensis* (3), called attention to the peculiar structure of the hyoid bone, and pointed out that "the thyro-hyal elements show but little curvature along their continuities, and still less disposition to curl up behind the cranium."

In 1891, Gadow (4) described the myology, neurology, and osteology of the Parrot's

[1] The two species of *Psittacus* described by Nitzsch are species of *Chrysotis* and *Ara*.

tongue: *Psittacus leucocephalus*, *Microglossus aterrimus*, and *Ara macao* were alone dealt with, and the account being comparative and incorporated with the description of the lingual myology of other birds, does not attempt to deal with the subject in an exhaustive or detailed manner.

In 1893, he (4′) divided the Parrots into two families, *i. e.*, Trichoglossidæ and Psittacidæ, basing his classification upon the external characters of the tongue, viz., the presence or absence of horny fibres (*Hornfasern*), the completeness or incompleteness of the orbital ring, and the direction of the file-like markings on the upper beak.

In 1895 and 1896 St. G. Mivart (6 & 7) published some very complete descriptions of the hyoid bones of various Parrots, and among others described and figured for the first time those of *Lorius domicella*, *Lorius flavo-palliatus*, and *Eos reticulata*. In this paper attention is directed to certain bony processes of which no previous records exist, and the relationships of these to certain muscles of the tongue I describe in the body of this paper.

Mivart further showed that the Order Psittaci is distinguished from every other order of birds by the shape of its hyoid, and that the characters which determine this are as follows:—

1. The posterior enlargement of the basihyal.
2. The growth upwards and forwards of a process on either side of the basihyal, which he proposed to call the parahyal process.
3. The presence of an os entoglossum (ceratohyal of Shufeldt) in the form either of a single broad bone with a considerable central foramen, or, much more commonly, of two lateral parts (entoglossals), which are united in their anterior middle region by cartilage so as to leave a space between this and their attachment to the basihyal.

He concluded that, among the Psittaci, the Loriidæ present a very distinctive character, in respect of the growth forward of the parahyal processes and their union in the middle line to form the parahyal arch; and in the course of this paper I am able to substantiate his conclusion, by the discovery that, in respect to their lingual muscles, the Loriidæ also present distinctive characters, in reference to which they appear to occupy an isolated position.

In 1893 Beddard and Parsons (5) called attention to certain points of similarity in the myology of Parrots, and directed attention to the existence of differences in the arrangements of the tendons of the tensor patagii muscle. Their observations led them to the conclusion that "the patagial tendons of *Psittacus* closely resemble those of *Chrysotis*"; and this is corroborated by certain facts embodied in the present paper, which show that a similar agreement exists between the two birds, in respect of a lingual muscle which, within the range of Parrots so far studied, exhibits certain modifications.

The outcome of the present investigation shows that the lingual muscles of Parrots are in the course of evolutionary changes, some of the muscles exhibiting the structural

variations indicative of these more markedly than others, and that the Loriidæ have advanced farthest along the road of specialization. These structural modifications are such that a series of graded stages, starting from the most primitive form and ending with the most specialized, can be determined.

Part II.—DESCRIPTION AND COMPARISON OF THE MUSCLES.

Ceratoglossus Muscle.

(a) *Inferior Ceratoglossus* (*basio-glossus of Nitzsch*).—This muscle exhibits a series of graded variations, and in one or two instances the variations are manifested among the species of the same genus and even upon either side of the same tongue. A comparison of its chief structural features shows that nine stages in the evolution of the muscle may be made out (*infra*, pp. 266 & 268), and that there are two types of structure, which I propose to call the "*unipars*" and "*duopars*" type. The unipars type is typically represented in the first stage, the duopars type in the highest stages, and the gradations from the one to the other in the intermediate stages.

Stage 1.

The most primitive form of the muscle is exhibited in *Cacatua alba*. It is inserted tendinous into the anterior lateral process of the os entoglossum, and arises fleshy from the posterior border of the basihyal and the margin of the whole length of the urohyal. Its general relations may be understood by reference to Pl. XXVIII. fig. 25, which represents its condition in *Cacatua galerita*. In particular, the extension of the muscular origin along the urohyal (UR.) appears to be a most primitive character, and in *C. alba*, *C. sulphurea*, and *C. triton* this is more strongly developed than in any other Parrot, extending as it does to the extremity of the bony portion. In *C. alba* the belly of this particular inner portion (*cg.i.a*^{1}.) of the muscle is more strongly developed than in any other species of *Cacatua*, the muscle of either side meeting each other, but not uniting, in the middle line considerably forwards, and remaining in contact throughout the remainder of their course backward to the extremity of their origin. The inner portion of the muscle is not in any way separated from the outer portion (*cg.i.a.*) as is partially the case in *C. galerita*, though there is a shallow groove indicative of the first stage towards the attainment of this condition. I propose to distinguish the whole of this muscle, which is almost exclusively related to the basihyal and entoglossum, and only extends backwards upon the hypobranchial as far as its head, as the *ceratoglossus inferior anticus* (*cg.i.a.*).

There is given off from the ventral surface of the outer portion of the muscle a muscular slip (*cg.i*^{1}.), which passes backward and becomes attached to a transverse tendon (*u.ten.*) that passes from the urohyal to the head of the hypobranchial.

I propose to call this muscle, which is very generally present, the *ceratoglossus inferior anticus accessorius* (*cg.i*^{1}.), and the tendon from which it arises as the *uro-hypobranchial tendon.*

The muscle, as a whole, does not possess a distinct tendon, but the fascia of its ventral surface is somewhat tendinous and anteriorly it is confluent with the similarly tendinous fascia of the lateral ceratoglossus (*cg.l.*). The absence of a distinct tendon is very characteristic of the more primitive forms of the muscle, and from the condition of the tendinous fascia here presented up to that of a strongly developed tendon in the more specialized forms there is every conceivable gradation. In *Cacatua roseicapilla* the muscle is like that just described, but the groove between the inner and outer portions of the muscle is here represented by a considerable thinning, so that these two portions are partially separated one from the other, and the thinned portion of muscle has developed a thin, flat, conical tendon whose apex is attached to the root of the urohyal; and the inner portion of the muscle (*cg.i.a*^{1}.) arises, not from the urohyal, but from the oval cartilaginous nodule (N.) which articulates with its ventral surface. In *Calyptorhynchus banksii* and *Calyptorhynchus funereus* the muscle resembles that in *Cacatua roseicapilla*, but differs from it in that the inner portion is inserted directly to the urohyal, as in *C. alba.* In *Ara ararauna* the muscle is fundamentally like that of *Cacatua alba*, but the inner portion (Pl. XXVIII. fig. 24, *cg.i.a*^{1}.) is less strongly developed, inasmuch as it does not extend on to the urohyal nor meet its fellow of the other side in the middle line. A ceratoglossus inferior anticus accessorius is absent.

Stage 2.

The muscle of the five species just described is typically that kind which I propose to name the *unipars type*; *i. e.*, it consists only of an anterior portion, which practically does not extend beyond the posterior border of the basihyal.

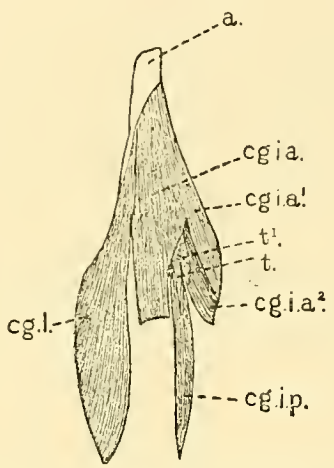
In *Cacatua galerita* the muscle is like that in *Cacatua alba*, but differs from it in that the inner portion (Pl. XXVIII. fig. 25, *cg.i.a*^{1}.) is partially separated from the outer (*cg.i.a.*) by a narrow area extended along the long axis of the muscle, in which the muscular tissue is thinned, but not to quite the same extent that it is in *Cacatua roseicapilla*; it further differs in the splitting of the ventral tendinous fascia into an inner and outer portion, which, however, still remain confluent in their anterior half, and in the extension backwards along the inner surface of the hypobranchial, for about the anterior fourth of the length of that, of a muscular tract (*cg.i.p*^{1}.) derived from, and continuous with, the outer portion (*cg.i.a.*) of the muscle. This small muscular tract shows no signs of dividing off from the parent muscle, and it is the first definite indication of the formation of a posterior portion of the muscle that reaches its maximum development in the Loriidæ. A glance at Pl. XXVIII. fig. 25 will show that the tendinous fascia is elongated backwards in such a way that it appears to

suggest an early stage in the formation of a tendon for this small muscular tract (*cg.i.p*^{1}.). In virtue of this posterior extension of the outer portion of the muscle it constitutes the second stage in its evolution, and inasmuch as the extended portion is continuous with the parent muscle it is still of the unipars type.

Stage 3.

In *Stringops habroptilus* a further advance is represented in the slightly greater extension of the muscular tract (Pl. XXVIII. fig. 26, *cg.i.p.*) along the hypobranchial, and more particularly in that this extended part has become severed from the muscular portion of the parent muscle (text-fig. 1, *cg.i.a.*), but is connected with that by

Text-fig. 1.



Stringops habroptilus.—Dorsal view of ceratoglossus inferior (right side). (Twice nat. size.)

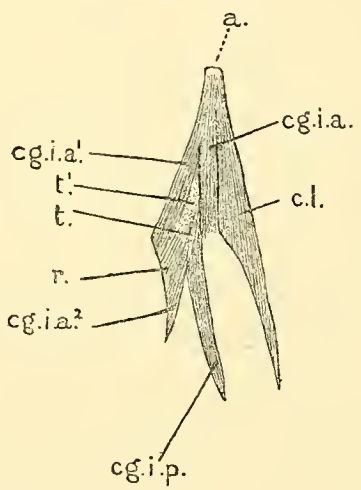
cg.i.a. = ceratoglossus inferior anticus.
cg.i.a'. = „ „ (inner portion of).
cg.l. = „ lateralis.
cg.i.a^2. = the portion of ceratoglossus inferior anticus which arises from the urohyal.
cg.i.p. = ceratoglossus inferior posticus.
t^1. = tendinous ventral fascia of *cg.i.a.*
t. = posterior prolongation of *t*^{1}.
a. = point of insertion of muscle to anterior lateral process of entoglossum.

attachment to a slender prolongation (*t.*) of its ventral fascia (*t*^{1}.). Thus, that which is but a posteriorly directed extension (*cg.i.p*^{1}.) of the outer portion of the parent muscle in *Cacatua galerita*, is here an independent muscle (*cg.i.p.*) with an origin from the fascia of the parent one and an insertion along the anterior third of the hypobranchial. I propose to speak of this muscle (*cg.i p.*), which reaches a much greater development in more specialized forms, as the *ceratoglossus inferior posticus*. The slender prolongation of the tendinous fascia to which it is attached, and which is

foreshadowed in *Cacatua galerita*, becomes in the higher stages evolved into a very pronounced tendon. The inner portion (*cg.i.a*^{1}.) of the ceratoglossus inferior anticus is strongly developed, but not quite so pronounced as that in *Cacatua* or *Calyptorhynchus*, nor does it, as in them, extend back to the extremity of the urohyal, but only along its anterior half; it is of uniform thickness, not exhibiting any area of retrogression, and its dorsal fascia also is slightly tendinous in its posterior region.

The muscle in *Cacatua leadbeateri* (text-fig. 2) is fundamentally like that in *Stringops*, but differs from it in the following details:—The ceratoglossus inferior posticus extends back along the hypobranchial through the anterior two-thirds, instead of only a third; the inner portion of the ceratoglossus inferior anticus (text-fig. 2, *cg.i.a*^{1}.) is thin in a region (*r.*) in such a way that a more posterior portion (*cg.i.a*^{2}.) related

Text-fig. 2.



Cacatua leadbeateri.—Ceratoglossus inferior, left side, dissected away from the hyoid bone and viewed from the dorsal surface, after a small portion of the ceratoglossus inferior anticus had been dissected away in order to reveal the tendinous fascia of the ventral surface. (Twice nat. size.) *r.*=retrogressing tract of *cg.i.a*^{1}. Other lettering as in text-fig. 1.

to the urohyal tends to become separated from a more anterior portion (*cg.i.a*^{1}.) related to the basihyal, and in which the former is attached to the tendinous prolongation (*t.*) that forms the origin of the ceratoglossus inferior posticus (*cg.i.p.*); the tendinous prolongation just referred to is attached to the ceratoglossus inferior posticus along the inner side of its dorsal surface, and not, as in *Stringops*, along the middle line; that portion of the ceratoglossus inferior anticus which arises from the urohyal takes its origin along the whole length of that, as in other species of *Cacatua*. A comparison of the condition of this muscle in *Cacatua leadbeateri* with that on the left-hand side of the tongue in *Ptistes erythropterus* (*infra*, p. 223, Pl. XXVIII. fig. 35) will show that

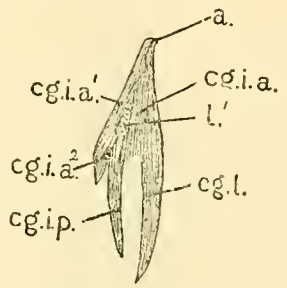
the exceptional condition of the latter is foreshadowed in that of the former, and that it could have arisen, and doubtless has arisen, by the completion of the incipient retrogression which is indicated in the region (*r.*, text-fig. 2), and by the development of the tendinous prolongation (*t.*) into a distinct tendon.

The muscle in *Cacatua sulphurea* is like that in *Cacatua leadbeateri*, but the ceratoglossus inferior posticus only extends along one-third of the length of the hypobranchial, in respect of which it resembles that in *Stringops*.

In *Calopsittacus novæ-hollandiæ* (text-fig. 3) the muscle is like that in *Stringops*, but the inner portion of the ceratoglossus inferior anticus is not so strongly developed.

In *Nasiterna pusio* the muscle is similar to that in *Stringops*, but the tendinous portion of the ventral fascia (Pl. XXIX. fig. 48) is restricted to a conical tract extending

Text-fig. 3.



Calopsittacus novæ-hollandiæ.—Dorsal view of ceratoglossus inferior (left side). A similar preparation to that of fig. 1. (Twice nat. size.) Lettering as in text-fig. 1.

from the insertion at the anterior lateral process, over the ventral surface of the anterior portion of the muscle, to its attachment to the ceratoglossus inferior posticus (posterior portion of the muscle) (*cg.i.p.*). The attachment of the latter portion of the muscle to this tendinous tract is somewhat more anteriorly situated than in *Stringops* or any other Parrot. The outer portion (*cg.i.a.*) of the ceratoglossus inferior anticus is more strongly developed in its lateral extension than in most instances, while the inner portion (*cg.i.a*^{1}.) does not extend back on to the urohyal.

The third stage is thus characterized by the fact that the posterior extension of the ceratoglossus inferior anticus of Stage 2 has separated from the parent muscle, but remains connected with that by attachment to a small prolongation of its ventral tendinous fascia, by the greater extension of the ceratoglossus inferior posticus along the hypobranchial, and by a slight retrogression of the urohyal origin of *cg.i.a*^{1}.

Stage 4.

This stage is characterized by a slight retrogression of the inner border and posterior extremity of the inner portion (*cg.i.a*^{1}.) of the ceratoglossus inferior anticus, and by the development in an antero-posterior direction, in the ventral tendinous fascia, of a very

slightly thickened tract that is prolonged backwards, and serves as an origin for the ceratoglossus inferior posticus (Pl. XXVIII. figs. 27 & 28). This tract is part of the substance of the ventral fascia of the muscle and cannot be separated from that without injury; it is not, therefore, an individual structure.

The ventral fascia of the muscle at this stage is still uniformly tendinous (Pl. XXVIII. figs. 27 & 28), and in its general features resembles that of the earlier stages.

In *Ara macao* (Pl. XXVIII. fig. 27) the ceratoglossus inferior posticus (*cg.i.p.*) extends along the hypobranchial (HB.) for the anterior third only, and the inner portion (*cg.i.a*^{1}.) of the ceratoglossus inferior anticus does not reach quite to the urohyal, but in other respects is well developed. Unlike that in *Ara ararauna*, there is a ceratoglossus inferior anticus accessorius (*cg.i*^{1}.). *Microglossus aterrimus* is similar to *Ara macao*, but the ceratoglossus inferior anticus accessorius is very small.

Cacatua triton, in respect of this muscle, is in its general features similar to other species of *Cacatua*, but in addition it possesses the characters which belong to this stage. It, however, deviates from this stage and belongs to that of the earliest in the great development of the inner portion (*cg.i.a*^{1}.) of the ceratoglossus inferior anticus, which is even more strongly developed than in *Cacatua alba*; it shows no signs of retrogression. The ceratoglossus inferior posticus extends backwards along the anterior third of the hypobranchial.

In *Cyanolyseus patagonicus* the muscle is like that in *Ara macao*, but the ceratoglossus inferior anticus accessorius (*cg.i*^{1}.) has almost disappeared.

In *Chrysotis ochrocephala* (Pl. XXVIII. fig. 28) the muscle resembles that of *Ara macao*, but the ceratoglossus inferior posticus (*cg.i.p.*) extends farther along the hypobranchial, reaching to the end of the anterior two-thirds, and the inner portion (*cg.i.a*^{1}.) of the ceratoglossus inferior anticus has undergone considerable retrogression in such a way that the lateral half of its inner part has disappeared. I propose to indicate this amount of retrogression by the numeral II; when, as in other cases, the whole of the inner portion has disappeared by the numeral III; when the extension on to the urohyal has disappeared and the inner lateral retrogression is not greater than in II, by I; and the fully developed muscle by O. The ceratoglossus inferior anticus accessorius (*cg.i*^{1}.) is very large, and arises from almost the whole length of the uro-hypobranchial tendon. In *Chrysotis panamensis*, *C. æstiva*, and *C. viridigena* the muscle is similar to that in *C. ochrocephala*, but the thickened tract in the tendinous fascia is slightly more pronounced, and tends to approach the condition of that in the next higher stage; the ceratoglossus inferior anticus accessorius is like that in *Ara macao*. In *C. panamensis* the ceratoglossus inferior posticus only extends one-half of the length of the hypobranchial, and the inner portion of the ceratoglossus inferior anticus is more strongly developed, not having retrogressed beyond stage I.

Stage 5.

In this stage the ventral fascia of the muscle is still tendinous, and to the same extent as that of the lower stages, but the thickened tract of Stage 4 has become slightly more pronounced, and has partially separated from the tendinous fascia, so that to a certain degree it is an individual tendon. There is also a very marked tendency for the ceratoglossus inferior posticus to extend back to the posterior extremity of the hypobranchial, and the retrogression of the inner portion of the ceratoglossus inferior anticus is becoming very pronounced, the muscles of some Parrots having reached almost complete retrogression (=III) in respect of this portion.

In *Psittacus erithacus* the muscle is typically represented at this stage. It is figured on Pl. XXVIII. fig. 29, and in its general features resembles that in *Chrysotis ochrocephalus*, from which it differs, in addition to the characters of the tendon, in that the ventral fascia is thicker (which cannot be well represented in a figure) and the inner portion of the ceratoglossus inferior anticus (*cg.i.a*^{1}.) sends back a small twig on to the head of the hypobranchial (HB.). The ceratoglossus inferior anticus accessorius (*cg.i*^{1}.) is of the usual type, and is not like that in *Chrysotis ochrocephalus*.

The muscle in *Coracopsis vasa* (Pl. XXVIII. fig. 31) is similar to that in *Psittacus*, but the inner portion (*cg.i.a*^{1}.) of the ceratoglossus inferior anticus is very strongly developed, and anteriorly, like that in *Ara macao*, it is covered with a tendinous fascia; it does not, like that in *Psittacus*, send back a small twig on to the hypobranchial. The ceratoglossus inferior posticus (*cg.i.p.*) extends along the hypobranchial for its anterior half only.

In *Palæornis torquata* (Pl. XXVIII. fig. 32) and *Psephotus xanthorrhous* the ceratoglossus inferior posticus reaches to the posterior limit of the hypobranchial; in the latter Parrot the inner portion of the ceratoglossus inferior anticus has quite disappeared (=stage III); but in *Palæornis* it has only attained to between this and II.

In *Conurus holochlorus*, *C. jendaya* (Pl. XXVIII. fig. 36), and *C. cactorum* (Pl. XXVIII. fig. 30) the ceratoglossus inferior posticus extends nearly the whole length of the hypobranchial. In the last of these three Parrots the inner portion of the ceratoglossus inferior anticus (*cg.i.a*^{1}.) is strongly developed, that of either side, turning inwards, becomes slightly separated from the outer part and meets its fellow in the middle line; in the first-named Parrot it has retrogressed almost to stage II, and in the second almost to stage III.

In *Deroptyus accipitrinus* the ceratoglossus inferior posticus extends a little more than the anterior two-thirds along the hypobranchial, and the inner portion of the ceratoglossus inferior anticus has retrogressed to stage II. The ceratoglossus inferior anticus accessorius resembles that in *Cacatua galerita* (Pl. XXVIII. fig. 25) in its mode of attachment to the uro-hypobranchial tendon—*i. e.*, it is attached to the ventral surface, instead of to its anterior margin as in the majority of Parrots.

In *Eclectus pectoralis* (Pl. XXIX. fig. 49) the ceratoglossus inferior posticus (*cg.i.p.*)

extends only one-half the length of the hypobranchial, and is continued forwards beyond the posterior edge of the basihyal to a greater extent than usual, in respect of which it resembles *Nasiterna*; the tendinous tract from which it arises is situated on its outer side and not along its middle line. The inner portion of the ceratoglossus inferior anticus (*cg.i.a*^{1}.) has reached stage II in its retrogression, and its posterior extremity is prolonged into a curved finger-like process; like that in *Coracopsis* and *Ara macao*, its anterior portion is covered with a tendinous fascia.

In *Brotogerys pyrrhopterus* (Pl. XXVIII. fig. 33) the muscle is different on either side of the tongue, that on the right having the general characters of this stage, in which the ceratoglossus inferior posticus extends to the posterior extremity of the hypobranchial, while the inner portion of the ceratoglossus inferior anticus has reached stage II of retrogression. On the left-hand side the ceratoglossus inferior posticus shows evidence of a retrogressive atavism, and has gone back to the condition of that in *Cacatua galerita* (Stage 2), in respect of the fact that it is represented by a posterior extension (*cg.i.p*^{1}.) of the ceratoglossus inferior anticus, which reaches back as far as the anterior third of the hypobranchial. Behind it there is an elongated conical muscle (*cg.i*^{3}.), originating by its apex from the posterior end of the ventral surface of the basihyal, and inserted by its base along the remaining two-thirds of the hypobranchial; it is not quite clear what this muscle represents, for, as far as its condition in *Brotogerys* is concerned, it might equally well be interpreted either as a part of the ceratoglossus inferior posticus or as a dorsal accessory ceratohyoideus. In *Psittinus incertus* (*infra* p. 227, & Pl. XXVIII. fig. 34) there is a similar condition, but here the muscle can be clearly seen to be a portion of the ceratoglossus inferior posticus, becoming separated from the parent muscle.

Stage 6.

In this stage the ventral fascia of the ceratoglossus inferior anticus, though still tendinous, is not so decidedly so as in the last stage, and the tendon derived from it is now more distinctly developed. The ceratoglossus inferior posticus in all cases, with one exception and another partial one, extends back to the posterior extremity of the hypobranchial, and, in respect of that, attains the highest condition of the muscle. In all cases, also, with but two exceptions, the inner portion of the ceratoglossus inferior anticus has attained either stage II or III in its retrogression.

In *Platycercus eximius* (Pl. XXIX. fig. 44) the muscle reaches its highest development for this stage, the specialized condition of that in *Pezoporus* excepted. The ceratoglossus inferior posticus extends backwards to the posterior limit of the hypobranchial (=$\frac{3}{3}$); the inner portion (*cg.i.a*^{1}.) of the ceratoglossus inferior anticus has quite disappeared (=III); the ventral fascia is only slightly tendinous, and the tendon derived from it is well developed; and the ceratoglossus inferior anticus accessorius (*cg.i*^{1}.) is relatively small. In *Pœocephalus rüppelli* the muscle is similar to that of *Platycercus*, but the ceratoglossus inferior posticus extends forwards a little beyond

the posterior margin of the basihyal, and the ceratoglossus inferior anticus is peculiar in that its origin is from the head of the hypobranchial, as well as from the posterior portion of the basihyal. In *Pœocephalus robustus* the muscle is almost identical with that of *P. rüppelli*, but the inner portion of the ceratoglossus inferior anticus has only reached stage II of retrogression. In *Bolborhynchus lineolatus* (Pl. XXIX. fig. 45) the muscle is similar to that in *Platycercus*, but the tendon of the ceratoglossus inferior posticus is slightly more pronounced and to a small extent spreads out in a fan-shaped form at its junction with the muscle; the inner portion of the ceratoglossus inferior anticus is also not the same, since it has only reached between stages II and III in its retrogression, and the ceratoglossus inferior anticus accessorius (*cg.i*^{1}.) is well developed. In *Tanygnathus mülleri* the muscle is very similar to that in *Bolborhynchus*, except that the tendon of the ceratoglossus inferior posticus is not quite so strongly developed; the inner portion of the ceratoglossus inferior anticus has not reached beyond stage II in retrogression, and upon the right side of the tongue it is prolonged backwards in the form of a little strip on to the hypobranchial, as in *Psittacus* (Pl. XXVIII. fig. 29) and *Ara macao*. In *Prioniturus* sp.? the muscle is like that in *Bolborhynchus*, but the inner portion of the ceratoglossus inferior anticus has not reached beyond stage II in retrogression.

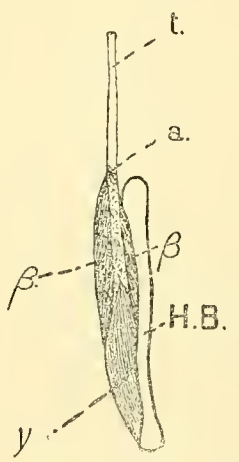
In *Pezoporus formosus* the muscle is very specialized, and were it not that the ventral fascia is still tendinous (Pl. XXIX. fig. 47) in its anterior portion, and that it possesses a remarkably well-developed ceratoglossus inferior anticus accessorius (*cg.i*^{1}.), I should have placed it in the highest stage with *Eos*. The inner portion of the ceratoglossus inferior anticus has quite disappeared. The tendon of the cerotoglossus inferior posticus is very strongly developed, as strongly as that in *Eos*, and the muscle itself is very big and divided into three portions. This division of the muscle is unique, and, if we except *Psittinus* and *Brotogerys*, in which the division is of another nature, does not occur in any other Parrot. The three parts into which it is divided lie one above the other ventro-dorsally; I propose to distinguish each as follows:— the *ceratoglossus inferior posticus ventralis* (Pl. XXIX. fig. 47, *a*), which arises from the tendon at the level of the anterior head of the hypobranchial and is inserted by a broad fleshy belly to the inner surface of the anterior two-thirds of the hypobranchial; the *ceratoglossus inferior posticus medius* (Pl. XXIX. fig. 47, & text-fig. 4, γ), arises from the extremity of the tendon and is inserted into the posterior third of the hypobranchial; and the *ceratoglossus inferior posticus dorsalis* (Pl. XXIX. fig. 47, & text-fig. 4, β), arises from the dorsal surface of the tendon from its posterior extremity to the level of the anterior head of the hypobranchial, and is inserted along the greater portion of the length of the hypobranchial. Of these, the *c. i. p. medius* is the stoutest and is oval in transverse section; the *c. i. p. dorsalis* is the longest, and is also almost as stout as the "medius"; while the *c. i. p. ventralis* is flat.

In *Psittinus incertus* (Pl. XXVIII. fig. 34) the muscle exhibits the characters of

this stage. The inner portion of the ceratoglossus inferior anticus has retrogressed to stage II. The ceratoglossus inferior posticus extends backwards nearly to the posterior extremity of the hypobranchial, and forwards a little anterior to the hinder margin of the basihyal; posteriorly it gives off a muscular strip (*cg.i*^{3}.) which passes inwards and forwards to the posterior border of the basihyal and near to the root of the urohyal (*cf. Brotygerys*, *ante* p. 221). This little strip is only found on the left-hand side of the tongue ; it is developing a very small tendon at its posterior extremity.

In *Ptistes erythropterus* (Pl. XXVIII. fig. 35) the inner portion of the ceratoglossus inferior anticus has retrogressed to stage II, and the ceratoglossus inferior posticus of the right side is like that in *Bolborhynchus*. On the left side it is very different, and the tendon gives origin to two divergently arranged muscles, the outer (*cg.i.p.*) of which is inserted to the anterior half of the hypobranchial, and the inner (*cg.i.a*^{2}.) to the

Text-fig. 4.



Pezoporus formosus.—Ventral view of a dissection of the left ceratoglossus inferior posticus to show the division of the muscle. The ventral layer (ceratoglossus inferior posticus ventralis=α) has been removed. (Thrice nat. size.)

H.B. = hypobranchial (left side).
t. = tendon of ceratoglossus inferior.
a. = anterior limit of the insertion of the ventral division of the muscle.
γ. = median division of the muscle.
β. = dorsal division of the muscle.

urohyal. It thus exhibits the completed stage of that condition which was foreshadowed in *Cacatua leadbeateri* (*cf. ante*, p. 217), and which could be reassumed if the inner portion of the ceratoglossus inferior anticus (*cg.i.a*^{1}.) were to grow backwards and become confluent with the urohyal portion (*cg.i.a*^{2}.) of the posterior ceratoglossus. A comparison of the two muscles leaves but little doubt that the urohyal portion (*cg.i.a.*^{2}) is a portion of the inner part of the ceratoglossus inferior anticus which has separated from that and secondarily become attached at an early stage to the tendon of the ceratoglossus inferior posticus. The early stage in this

separation, and the secondary attachment of the muscle to the tendon, is actually seen in *Cacatua leadbeateri*. Why the assumption of this particular condition should be confined to the left side, or why the asymmetrical departure should always occur on the left side, is a question which the present range of facts cannot answer.

In *Nestor notabilis* (Pl. XXIX. fig. 46) the ceratoglossus inferior posticus (*cg.i.p.*) only extends back along the anterior two-thirds of the hypobranchial, and its tendon is very strongly developed. A ceratoglossus inferior anticus accessorius is absent.

Stage 7.

In this stage the ventral fascia of the ceratoglossus inferior anticus is no longer tendinous, as a consequence of which the tendons of the ceratoglossus inferior posticus and ceratoglossus lateralis are independent, except at their common origin at the anterior lateral process. The tendon of the ceratoglossus inferior posticus is slightly more strongly developed than in the earlier stage, and without a single exception the muscle itself extends back to the posterior limit of the hypobranchial ($=\frac{3}{3}$). The inner portion of the ceratoglossus inferior anticus has completely disappeared (=III) in about one-half of the muscles examined.

In *Pyrrhura leucotis* (Pl. XXIX. fig. 40) the muscle exhibits the highest characters of this stage, *i. e.*, the tendon is well developed and spreads out to a small degree in a fan-shaped form at its attachment to the ceratoglossus inferior posticus; the latter extends along the whole length of the hypobranchial, and the inner portion of the ceratoglossus inferior anticus has disappeared. In *Nymphicus uvæensis* and *Cyanorhampus auriceps* the muscle is similar to that in *Pyrrhura*. In *Loriculus galgulus* (Pl. XXIX. fig. 42) the inner portion of the ceratoglossus inferior anticus persists as a small vestige (=between II & III) and smaller posteriorly than anteriorly. The tendon spreads out in a fan-shaped form upon the ventral surface of the ceratoglossus inferior posticus at its junction with that, and upon the dorsal surface it runs back as a narrow tract, similar to that on the ventral surface of the muscle in *Lorius flavo-palliatus* (Pl. XXIX. fig. 38). In *Psittacula passerina* the muscle (Pl. XXIX. fig. 41) is similar to that in *Pyrrhura*, except that the inner portion of the ceratoglossus inferior anticus is like that in *Loriculus*. The ceratoglossus inferior anticus accessorius (*cg.i*^{1}.) is supplemented by a second one (*cg.i*^{2}.), which arises not from the parent muscle itself, but from its tendon. I propose to call it the *ceratoglossus inferior anticus accessorius secundus*. In *Caica leucogaster* the muscle is similar to that in *Pyrrhura*, though the tendon is somewhat thinner, and the inner portion of the ceratoglossus inferior anticus persists, and for this stage is strongly developed (=II).

In *Pyrrhulopsis splendens* the muscle exhibits several peculiarities: the inner portion of the ceratoglossus inferior anticus is almost primitive on the left side, since it reaches to the middle line as in *Ara macao* (Pl. XXVIII. fig. 27) (= I), but on the right side it has retrogressed to stage II; and anteriorly, that of the latter side

sends forwards a small muscular tract which becomes confluent with the outer border of the right hypoglossus rectus, very similar to that in *Stringops* (Pl. XXVIII. fig. 26), but differing from it in its partial separation from the parent muscle and in its greater size. The fibres of the ceratoglossus inferior posticus are sagittally arranged, the tendon extending backwards for some distance between the two rows of converging fibres; the sagittal arrangement is very similar to that of the ceratoglossus inferior posticus dorsalis of *Pezoporus* (Pl. XXIX. fig. 47, β, & text-fig. 4, p. 223). Were the inner row of fibres to lose its connection with the tendon and to become attached by its anterior extremity to the posterior margin of the basihyal, the muscle would repeat the condition exhibited by that of the left-hand side in *Brotogerys* and *Psittinus*, assuming that, coincidently with the separation from the tendon, the fibres slightly altered their direction.

In *Pyrrhulopsis personata* the muscle is similar to that in *P. splendens*, but the ceratoglossus inferior anticus is the same on both sides, resembling the right-hand one of the latter bird, but not possessing the anterior extension to the hypoglossus; and the fibres of the posterior ceratoglossus are not so markedly sagittate in their arrangement.

Stage 8.

As in the lower stage (7) the ventral fascia of the ceratoglossus inferior anticus is not tendinous, but the tendon is much more strongly developed and extends farther posteriorly along the ceratoglossus inferior posticus. The latter muscle is always strongly developed and reaches to the posterior extremity of the hypobranchial. The inner portion of the ceratoglossus inferior anticus in two of the three instances examined has undergone complete retrogression (= III). A ceratoglossus inferior anticus accessorius is absent.

In *Lorius domicella* (Pl. XXIX. fig. 37) the fascia of the ceratoglossus inferior posticus (*cg.i.p.*) at the posterior extremity of the muscle is tendinous, and the muscle itself is not attached, except by connective tissue, along the whole surface of the hypobranchial; the tendinous fascia is thus probably correlated with the loss of power resulting through a reduction of attaching surface. Posteriorly the muscle is merged with the posterior portion of the superior ceratoglossus. The ceratoglossus inferior anticus (*cg.i.a.*) is relatively small and tends to divide into a ventral inner and a dorsal outer portion; its inner portion has practically reached stage III in retrogression. In *Lorius flavo-palliatus* (Pl. XXIX. fig. 38) the ceratoglossus inferior anticus does not tend to split into two portions and its inner part has only reached stage II in retrogression. The ceratoglossus inferior posticus is somewhat stouter than in *L. domicella*, and the tendon runs back upon its mid-ventral surface for about half its length. In *Vini australis* the muscle is similar to that in *Lorius domicella*, except that the origin of the ceratoglossus inferior posticus is like that in *L. flavo-palliatus*, and the ceratoglossus inferior anticus does not split into two portions.

Stage 9.

This stage differs from the last only by the marked manner in which the posterior end of the tendon spreads out in a fan-shaped form (Pl. XXIX. fig. 39) over the anterior half of the ceratoglossus inferior posticus.

Eos riciniata is the only one of the Parrots examined that exhibits this particular character developed to the same extent. The ceratoglossus inferior anticus is merged with the lateral ceratoglossus along its whole length, except where the uro-hypobranchial tendon passes between them to its attachment at the basihyal; its inner portion has completely retrogressed (= III). The ceratoglossus inferior posticus is like that in *Lorius flavo-palliatus*.

(b) *Lateral Ceratoglossal.*—This muscle arises fleshy from the dorso-lateral surface of the hypobranchial and is inserted by a tendinous insertion, common to it and the inferior ceratoglossal, to the anterior lateral process of the os entoglossum. In some cases its origin posteriorly is from the dorsal surface of the hypobranchial, and it gradually shifts, as it runs forwards, to the lateral surface. The chief differences which it exhibits are concerned with the amount of its extension along the hypobranchial, in its confluence or separation from the ceratoglossus inferior anticus, and in the nature of its tendon, *i.e.*, as to whether it is a distinct tendon or merely a tendinous fascia. With respect to the last character, the tendon varies in precisely the same way and in correlation with that of the inferior ceratoglossal, being a distinct tendon when that of the latter is so, and of the nature of a tendinous fascia otherwise; in the cases where it is of the latter description, the two muscles are covered by a single fascia, and the tendon of the lateral ceratoglossal, like that of the inferior ceratoglossal, is evolved as a thickened tract, the progress of its evolution keeping pace with that of the latter muscle.

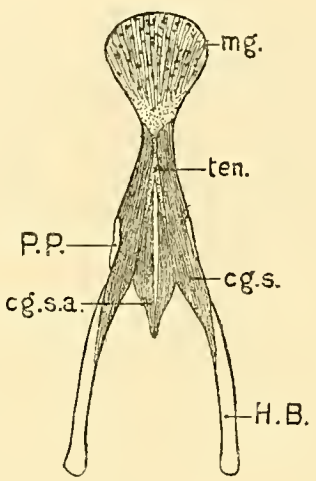
In *Cacatua alba*, *C. leadbeateri*, and *Calyptorhynchus funereus* the muscle extends backwards along the anterior third of the hypobranchial; in the last-named Parrot it is slightly more than this. In *Ara*, *Cyanolyseus*, *Cacatua triton*, *C. sulphurea*, *C. roseicapilla*, *C. galerita* (Pl. XXVIII. fig. 25), *Calyptorhynchus banksi*, *Deroptyus*, *Microglossus*, *Nasiterna*, *Nestor*, *Psittacus* (Pl. XXVIII. fig. 29), *Psittacula*, *Psephotus*, *Pœocephalus robustus*, and *Stringops* (Pl. XXVIII. fig. 26) it extends along the anterior half. In *Coracopsis*, *Chrysotis panamensis* (Pl. XXVII. fig. 14), *C. æstiva*, *C. viridigena*, *Calopsittacus*, *Pœocephalus rüppelli*, *Tanygnathus*, *Nymphicus*, *Conurus cactorum*, *Erotogerys*, *Palæornis* (Pl. XXVIII. fig. 32), *Pyrrhulopsis*, and *Loriculus* it extends along the anterior two-thirds. In *Psittinus*, *Chrysotis ochrocephala* (Pl. XXVIII. fig. 28), and *Pionopsittacus* it is just slightly more. In *Lorius* (Pl. XXIX. fig. 37), *Eos* (Pl. XXIX. fig. 39), *Vini*, *Cyanorhamphus*, *Prioniturus*, *Conurus holochlorus*, *C. jendaya*, *Pyrrhura*, *Caica*, *Pezoporus*, *Ptistes*, *Bolborhynchus*, *Platycercus*, and *Eclectus* it extends to or near the posterior extremity of the bone. In *Platycercus* and *Eclectus* the muscle turns to the dorsal surface in its posterior

two-thirds. In *Cacatua galerita*, *C. roseicapilla*, *Calyptorhynchus banksi*, *Conurus jendaya*, *C. cactorum*, *C. holochlorus*, *Psephotus*, *Platycercus*, *Pœocephalus robustus*, *Bolborhynchus*, *Psittinus*, *Palæornis*, *Psittacula*, *Cyanorhamphus*, *Nymphicus*, *Ara macao*, *Nestor*, and *Eos* the muscle is confluent with the ceratoglossus inferior anticus. In *Cyanolyseus*, *Microglossus*, *Pyrrhura*, *Caica*, *Ptistes*, *Tanygnathus*, *Pœocephalus rüppelli*, *Deroptyus*, *Psittacus*, *Coracopsis*, *Ara ararauna*, and *Cacatua sulphurea* there is an incipient division commencing, usually more marked at the posterior end. In *Calopsittacus*, *Chrysotis viridigena*, *C. ochrocephala*, *C. panamensis*, *Lorius flavopalliatus*, *Pionopsittacus*, *Cacatua alba*, *C. leadbeateri*, *C. triton*, *Prioniturus*, *Stringops*, *Pyrrhulopsis*, *Loriculus*, and *Vini* the division of the two muscles is more or less distinctly indicated in the posterior half of their common course. In *Lorius domicella*, *Pezoporus*, and *Eclectus* the two muscles are divided, more or less, along their whole common course. In such forms as *Cacatua* and *Stringops*, where the fascia is continuous and tendinous, the division is only apparent when the muscle is dissected away and examined from the dorsal surface. Even then the division is not so pronounced as in the other muscles with distinct tendons, and is hardly comparable with them, since the fascia remains undivided.

(c) *Superior Ceratoglossal.*—This muscle is exhibited in its primitive form in *Cacatua*, *Ara ararauna*, *Calyptorhynchus*, and *Calopsittacus*. In *Cacatua galerita* (Pl. XXVII. fig. 13) the muscle arises from the dorso-inner surface of the anterior half of each hypobranchial, and passing forwards and slightly inwards over the dorsal surface of the basihyal, from which it also in part arises, becomes inserted into the thick sheath investing a conical mass of dense connective tissue (*mg*^{1}.) that lies in the dorsal concavity of the entoglossum (EN.). In a large number of Parrots this conical mass of tissue is either entirely replaced by muscle or by a mixture of muscle and connective tissue; and I propose to speak of it when muscular as the *mesoglossus muscle* (*mg.*), and when otherwise as the *mesoglossus tissue* (*mg*^{1}.). In *Cacatua galerita* the two halves of the superior ceratoglossus become confluent just before reaching their insertion, and each narrows somewhat as it passes forwards from its origin. In *Cacatua leadbeateri*, *C. alba*, and *C. sulphurea* the muscle is like that in *C. galerita*. In *C. triton* the two halves each receive a small bundle of auxiliary fibres which arise from the basihyal at the roots of the parahyal processes. In *Calopsittacus novæhollandiæ* the muscle differs from that in *Cacatua galerita* in that its origin extends farther back upon the hypobranchial, and in *Coracopsis vasa*, *Nymphicus uvæensis*, and *Psephotus xanthorrhous* in that it does not extend beyond the anterior third. In *Calyptorhynchus funereus* the muscle is like that in *Cacatua galerita*, but in *Calyptorhynchus banksi* it arises from the anterior fifth only of the hypobranchial, and from the insertion of the muscle (text-fig. 5, *ten.*) there runs backwards a bifid tendon, each fork of which extends for a short way only along the inner side of each half of the muscle; to the inner side of each of the latter there is a small muscular bundle (*cg.s.a.*)

given off, each possessing an independent origin along the anterior half of the dorso-lateral surface of the urohyal, and which I shall allude to as the *ceratoglossus superior accessorius*. The condition of the muscle which is exhibited in this Parrot is very similar to that in *Psittinus incertus* (text-fig. 5, *cg.s.*, *cg.s.a.*, *ten.*). In *Cacatua roseicapilla* the muscle in respect of its origin and insertion is like that in *Cacatua galerita*, but resembles *Calyptorhynchus banksi* in the possession of a ceratoglossus superior accessorius, from which it differs, however, because the origin of this extends the whole length of the urohyal and it is almost completely separated from the parent

Text-fig. 5.



Psittinus incertus.—Dorsal view, to show the connection of the ceratoglossus superior with the mesoglossus and the formation of an accessory muscle (*cg.s.a.*), partially separated from the parent one by a bifid tendon (*ten.*). (Thrice nat. size.)

Additional letters.

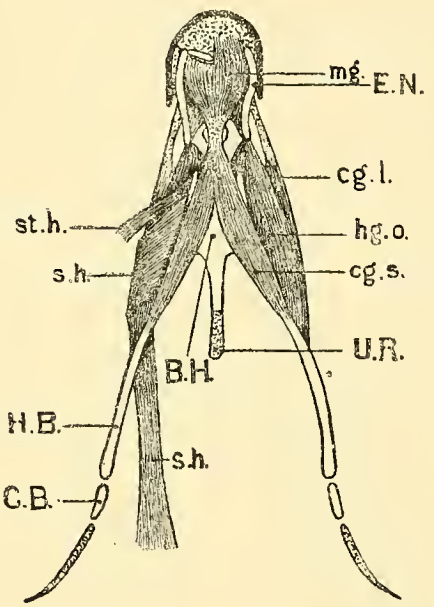
cg.s. = ceratoglossus superior.	*mg.* = mesoglossus.
cg.s.a. = „ „ accessorius.	P.P. = parahyal process.
H.B. = hypobranchial.	*ten.* = tendon.

muscle. In *Pyrrhura leucotis* (Pl. XXVII. fig. 19) the muscle is similar to that in *Cacatua galerita*.

In *Stringops habroptilus* (Pl. XXVII. fig. 18) the origin of the muscle extends back to the anterior third only of the hypobranchial, and in the possession of a bifid tendon running backwards from its insertion it is similar to that in *Calyptorhynchus banksi*, though it is much more strongly developed. A ceratoglossus superior accessorius (*cg.s.a.*) like that in *Cacatua roseicapilla* is present, but differs slightly from that in its insertion to the crura of the bifid tendon, instead of to the muscle itself, so that it is otherwise completely separated from the parent muscle.

In *Ara ararauna* (text-fig. 6) the muscle is like that in *Cacatua galerita*, but it passes over the basihyal without forming an origin from it. In *Ara macao* the muscle is similar to that in *A. ararauna*, but the two halves are distinct right up to their insertion and a rudimentary bifid tendon is present (Pl. XXVII. fig. 20, *cg.s.*). In *Microglossus aterrimus* it is like that in *Ara ararauna*, but there appears to be an additional insertion to the dorsal concavity of the rounded anterior extremity of

Text-fig. 6.



Ara ararauna.—Dorsal view. The trachea, thyrohyoideus and thyroglossus have been removed, and upon the right, also the stylohyoideus and sternohyoideus and a part of the anterior portion of the mesoglossus, in order to show the rounded cartilaginous extremity of the entoglossum, over which the sheath of the muscle works. (Nat. size.)

Additional letters.

B.H. = basihyal.	*hg.o.* = hypoglossus obliquus.	*st.h.* = sternohyoideus.
C.B. = cerato-branchial.	*s.h.* = stylohyoideus.	U.R. = urostyle.
E.N. = entoglossum.		

the basihyal, which lies immediately ventrad of the usual insertion (*cf.* Mivart, P. Z. S. 1895 and 1896).

In *Chrysotis ochrocephala* (Pl. XXVII. fig. 12) and *Deroptyus accipitrinus* the muscle is similar to that in *Cacatua galerita*, but its origin along the hypobranchial is not quite so extensive, and anteriorly it receives on either side a small bundle of fibres arising from the ventral surface of the hyoid, and which appears to be a portion of the hypoglossus obliquus forming a new connection. In *Chrysotis* (*viridigenalis*)

viridigena there is a rudimentary bifid tendon a little smaller than that in *Conurus jendaya* (Pl. XXVI. fig. 9), but otherwise similar. In *Chrysotis panamensis* (Pl. XXVII. fig. 14) there is an unpaired ceratoglossus superior accessorius (*cg.s.a.*) arising from the left-hand parent muscle and attached to the root of the urohyal. In *Chrysotis æstiva* the attachment of the muscle to the fascia of the mesoglossus is unique; a small triangular cartilage, having rounded ventral and dorsal surfaces, is fixed by its base to the mesoglossus, while its other two sides form an insertion for the two halves of the superior ceratoglossus, each to each. The position of this cartilage with respect to the hyoid bone is immediately dorsad of the slight concavity in the rounded extremity of the basihyal. Apparently this concavity is present in the hyoid bones of all Parrots so far examined (*cf.* Mivart, P. Z. S. 1895 and 1896), but no meaning can be attached to its presence. So far as this Parrot is concerned, this little cartilage explains the concavity, for together they form a shallow ball-and-socket joint arrangement. The cartilage is present in no other Parrot, while the concavity is almost generally so. There is also present a bifid tendon, similar in its relation and strength of development to that in *Conurus jendaya* (Pl. XXVI. fig. 9). In *Nasiterna pusio* the muscle is like that in *Chrysotis ochrocephala*, but does not possess the lateral bundle of fibres on either side.

In *Pyrrhulopsis splendens* and *P. personata* the muscle is like that in *Chrysotis ochrocephalus*, but the muscle is splitting posteriorly into a larger dorsal and a smaller ventral bundle; the former arises from the hypobranchial, and the latter from the basihyal.

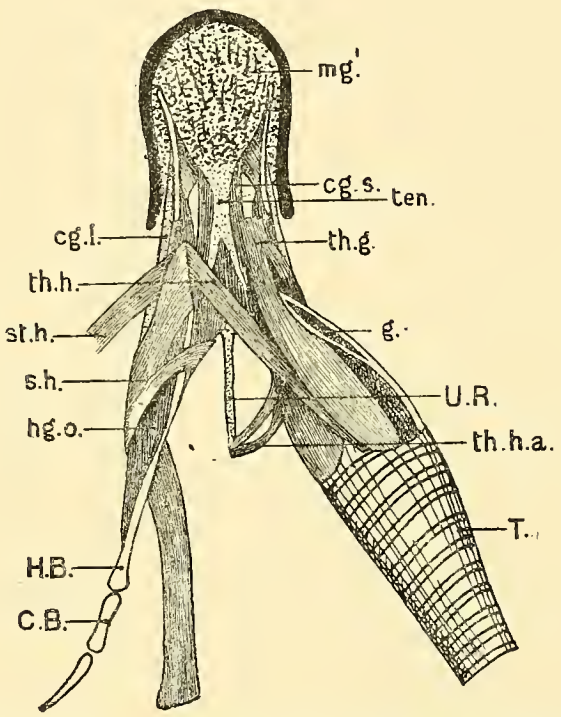
In *Psittacus erithacus* (Pl. XXVII. fig. 15) the muscle extends back along the anterior half of the hypobranchial, but at that point where is its insertion in other Parrots it is continuous with the mesoglossus muscle, and is not inserted into the fascia of that, as in other Parrots.

In *Conurus jendaya* (Pl. XXVI. fig. 9) the muscle arises, as in *Stringops*, from the anterior third only of the hypobranchial, and it possesses a bifid tendon of insertion, the rami of which extend along the middle of each muscle, and not along the inner side as in *Stringops* and *Psittinus*. There is present on the right side only a ceratoglossus superior accessorius (*cg.s.a.*)—a unilateral condition similar to that in *Chrysotis panamensis*, but occurring on the opposite side of the tongue. In *C. cactorum* it is like that in *C. jendaya*, but there is no accessory muscle. In *C. holochlorus* as in *C. cactorum*, but the bifid tendon is more strongly developed than in any other species of *Conurus*. In *Cyanolyseus patagonicus* and *Loriculus galgulus* as in *C. cactorum*, but there is no bifid tendon. In *Pinopsittacus pileatus* as in *Conurus cactorum*.

In *Eclectus pectoralis* (text-fig. 7) the origin of the muscle is from the anterior fifth only of the hypobranchial, and the bifid tendon of insertion is very broad, its rami extending backwards over the dorsal surface, in the mid-line of each half of the muscle.

In *Palæornis torquata* (Pl. XXVI. fig. 7), *Pæocephalus rüppelli*, and *Pæocephalus robustus* the origin of the muscle extends almost to the posterior extremity of the hypobranchial; in both, the bifid tendon is similar to that in *Eclectus*, but it is not so strongly developed, and less so in *Pæocephalus* than *Palæornis*. In *Ptistes erythropterus* the muscle is similar to that in *Pæocephalus*, but its origin only extends halfway along the hypobranchial.

Text-fig. 7.



Eclectus pectoralis.—Dorsal view. The trachea (T.) has been turned to the right and only sufficient of the stylohyoideus (*st.h.*) left to show its insertion. (Twice nat. size.)

Additional letters.

g. = glottis.	*th.g.* = thyroglossus.	*th.h.a.* = thyrohyoideus
T. = trachea.	*th.h.* = thyrohyoideus.	accessorius.

In *Platycercus eximius* (Pl. XXVI. fig. 11), *Pezoporus formosus* (Pl. XXVI. fig. 8), *Prioniturus* sp.?, *Cyanorhamphus auriceps*, and *Tanygnathus mülleri* the tendon of insertion is bifid and is similar to that in *Conurus jendaya*, but its anterior portion is more or less distinctly cylindrical and slightly elongated, and it foreshadows the markedly cylindrical tendon of the Loriidæ (Pl. XXVII. fig. 21, *ten.*).

In *Psittacula passerina*, *Caica leucogaster*, and *Bolborhynchus lineolatus* the muscle arises from the anterior third of the hypobranchial and is inserted by a cylindrical tendon to the mesoglossus; the tendon is not bifid.

In *Lorius domicella* (Pl. XXVII. fig. 21) the muscle attains its highest development, its origin extending along the whole length of the hypobranchial and at the posterior extremity of which it is slightly tendinous. Along the posterior two-thirds of its hypobranchial connection it is fused with the dorsal surface of the ceratoglossus inferior posticus. In the basihyal region it splits into a smaller ventral layer (*cg.ss.*), and a larger dorsal one (*cg.s.*), of which the former has its origin from the basihyal and the latter from the hypobranchial. The condition of the divided muscle is foreshadowed in *Pyrrhulopsis* (*cf. ante*, p. 230). Anteriorly the two pairs of muscles become confluent and merge with an elongated markedly cylindrical tendon (*ten.*) that inserts them to the mesoglossus; the tendon lies immediately ventrad of the symphysis of the parahyal arch. In *Vini australis* the muscle is similar to that in *Lorius domicella*, but the ceratoglossus subsuperior (*cg.ss.*) is more strongly developed and extends back as far as the base of the urohyal; the muscle is merged with the ceratoglossus inferior posticus at its posterior extremity only. In *Lorius flavo-palliatus* and *Eos riciniata* there is no splitting of the muscle; in other respects it is similar to that of *L. domicella*.

In *Nestor notabilis* (Pl. XXVII. fig. 22) the muscle arises from the anterior third of the hypobranchial and the two halves remain distinct throughout; their tendon is flat and elongated and extends forward to the anterior extremity of the tongue, where it becomes connected with the tendons of the hypoglossus rectus and with the covering membrane of the tongue. This elongated tendon probably represents in part the fascia of the mesoglossus; for in *Nestor* the mesoglossus muscle itself has disappeared.

Thyrohyoideus and Thyrohyoideus accessorius Muscles.

The thyrohyoideus, apart from its connection with the thyroglossus, exhibits very constant characters in all the Parrots examined. In the majority of them it arises from the anterior portion of the parahyal process and is inserted into the ventrolateral surface of the thyroid. In some it gives off upon its inner side a small muscular branch, but as this is a rudiment of the thyroglossus, variations of this sort will be considered under that muscle.

In *Cacatua roseicapilla* and *C. galerita* (Pl. XXVII. fig. 13, *th.h.*) the muscle exhibits the most primitive condition, and there is given off from the ventral edge of the thyrohyoideus a relatively large branch (*th.h.a.*) which is attached to the basihyal at the base of the urohyal; in other Parrots this becomes more or less separated from the parent muscle, and I propose to speak of it as the *thyrohyoideus accessorius*. It is slightly smaller in *C. roseicapilla* than in *C. galerita*. In *C. leadbeateri* the accessory muscle is smaller, but it is partially divided into two anteriorly, and the posterior of the two branches thus formed has shifted its origin to the head of the hypobranchial. In *C. alba*, *Calyptorhynchus funereus*, and *Calyptorhynchus banksi* the muscle is like that in *C. leadbeateri*, but the posterior branch of the accessory muscle arises from the basi-

hyal near the root of the urohyal; the accessory muscle is much more strongly developed. The muscle in *C. triton* is like that in *C. alba*, but the division of the accessory muscle is not so well marked and appears to be incipient rather than actual. In addition, there is present on the left side a very narrow muscle that arises from the extremity of the cartilaginous continuation of the urohyal and is inserted into the fourth tracheal ring; in its origin and narrowness it resembles a similar muscle in *Eclectus* (text-fig. 7, *th.h.a.*, p. 231), but differs from it in its insertion. In *C. sulphurea* the thyrohyoideus is divided into two, the anterior division arising from the apex of the parahyal process and the posterior one from the posterior half; both are inserted into the ventro-lateral surface of the thyroid. The thyrohyoideus accessorius consists of two divisions, the origins of which have been shifted forward to the cylindroidal portion of the basihyal and are inserted to the posterior end of the thyroid. The muscle is therefore more complex than in other species of *Cacatua*, and the origin of the accessory muscle is much more anterior. In *Calopsittacus novæ-hollandiæ* the muscle resembles that in *Cacatua alba*, but the accessory muscle is divided into four narrow bundles, the collective origin of which is nearly the same as that of the two bundles in *C. alba*, but has a slightly more posterior extension, since the hindmost two of the four arise from the lateral surface of the anterior end of the urohyal.

In *Eclectus pectoralis* (text-fig. 7, p. 231), *Pœocephalus robustus* [1], and *Nasiterna pusio*, the accessory muscle exhibits an unusual arrangement. It is very narrow, and arises, not from the basihyal, but from the posterior extremity of the urohyal, and is inserted at the anterior end of the thyroid. In *Nasiterna* it widens very much at its insertion. In *Stringops habroptilus* (Pl. XXVII. fig. 18) and *Microglossus aterrimus* the accessory muscle (*th.h.a.*) is quite separated from the parent one, and its origin is from the posterior edge of the basihyal and the outer margin of the urohyal; its insertion is partly to the posterior border of the thyroid and partly to the first tracheal ring behind that. In *Microglossus* the thyrohyoideus extends forwards beyond its origin at the parahyal process as a small muscular tract, which forms a second origin at the posterior extremity of the entoglossum; the tract on the right side is about three times as large as that on the left. In *Nestor notabilis* (Pl. XXVII. fig. 22) the thyrohyoideus arises from the posterior two-thirds of the parahyal arch and to a small extent from the dorsal surface of the body of the hyoid; the extension of the origin backwards on to the basihyal is suggestive of one of a primitively more extensive nature. The thyrohyoideus accessorius is like that in *Stringops* and *Microglossus*, except that at its origin the muscle is narrowed. There is also present a muscle which I have not found in any other Parrot: it arises from the sheath investing the urohyal, turns outward and runs over the surface of the ceratohyoideus, round the lateral ceratoglossal to the dorsal surface of the tongue, thence over the sternohyoideus and thyroglossus

[1] But not in *P. rüppelli*.

to the edge of the glottis, into the anterior two-thirds of which it is inserted. It has advanced very far in its retrogression, and consists only of the fascia with a few muscular fibres; I shall speak of it as the *thyrohyoideus accessorius transversalis* (Pl. XXIX. fig. 46, *th.h.a.t.*).

In all the species of *Conurus*, *Chrysotis*, *Ara*, *Deroptyus*, and *Cyanolyseus* the muscle is narrow at its origin and widens at its insertion. In *Conurus jendaya* (Pl. XXVI. fig. 9) and *C. holochlorus* the muscle is merged with the thyroglossus at its posterior end [1]; in *Cyanolyseus patagonicus* and *Pyrrhura leucotis* (Pl. XXVII. fig. 19) the confluence is greater, and in *Conurus cactorum* the two muscles are represented by a single one with a double origin, which is very similar to that in *Brotogerys* (text-fig. 9, p. 238, *th.h.*, *th.g.*). In *Chrysotis*, *Deroptyus*, and *Ara* the muscle, though lying in contact with the thyroglossus in its posterior region, is not confluent with it at any part. In *Psittacus* (Pl. XXVII. fig. 15) and *Coracopsis* (Plate XXVII. fig. 17) the thyrohyoideus is hidden by the thyroglossus, which overlies it somewhat dorso-laterally, and in the latter bird it is narrowed at its origin. In *Psittacula* and *Pezoporus* (Pl. XXVI. fig. 8) there is a like condition, but the thyroglossus lies wholly dorsally to the thyrohyoideus. In *Palæornis* (Pl. XXVI. fig. 7) the thyrohyoideus is very thin and narrow; it is slightly stouter in *Tanygnathus*; and in *Loriculus galgulus* (Pl. XXVII. fig. 23), in addition, it narrows very considerably at its insertion. In *Bollorhynchus* the relation of the muscle to the thyroglossus is similar to that in *Platycercus* (Pl. XXVI. fig. 11), but it is confluent with that at its origin and insertion, and separated in the intervening portion of its course. In *Pyrrhulopsis splendens* and *P. personata* the thyrohyoideus arises from the inner surface of the parahyal process anterior to the insertion of the stylohyoideus on the outer surface; in most Parrots the two muscles are attached opposite each other.

In *Cyanorhamphus*, *Prioniturus*, *Caica*, *Ptistes*, *Nymphicus*, and *Psephotus* there are no special features worthy of notice.

In *Pionopsittacus pileatus* a thyrohyoideus is absent. In *Psittinus incertus* the muscle is also absent, unless one which has the insertion of a thyrohyoideus, but the origin of a thyroglossus, be regarded as the muscle which has changed its origin.

The absence of the muscle in *Pionopsittacus* and its attenuation in others would seem to indicate that in some it is undergoing retrogression.

In *Lorius domicella* (Pls. XXVII. & XXIX. figs. 21 & 50) and *L. flavo-palliatus* the muscle arises from the anterior end of the crura of the parahyal arch, immediately behind the hypocleidium, and is inserted in a somewhat oblique fashion into the dorso-lateral surface of the thyroid, being covered at its insertion by the thyroglossus. In *Eos riciniata* the muscle is similar in its relations, but it is confluent at its origin with the thyroglossus. In *Vini australis* the muscle is confluent both at its origin and insertion with the thyroglossus, though free elsewhere.

[1] The artist, however, has represented the two muscles as distinct at their posterior extremity.

Thyroglossus Muscle.

The condition which this muscle exhibits is interesting. Its evolution starts from three distinct initial stages, all of which meet at a higher stage by convergence, and thence pass to the still higher ones by a common road. The evidence shows that the thyroglossus has arisen from the thyrohyoideus, and that it has done so by three methods: (A) the thyroglossus arises as a branch which separates from the thyrohyoideus as soon as the plane of division is formed, the latter commencing at the anterior end and gradually extending posteriorly; (B) the plane of division is formed in the parent muscle (thyrohyoideus), but the thyroglossus does not immediately separate from it; (C) the thyroglossus arises as a forward extension of a portion of the thyrohyoideus, which grows forwards to form an origin at the entoglossum without first separating from the parent muscle.

Method A.

Stage 1.

Cacatua roseicapilla and *Cacatua leadbeateri* exhibit the first stage by this method. In these birds the muscle is represented by a small branch separating from the anterior portion of the thyrohyoideus; the branch has lost its origin at the parahyal process and its free extremity does not extend beyond the level of the anterior extremity of the thyroid; the branch is slightly larger in *C. leadbeateri* than in *C. roseicapilla*.

Stage 2.

In *Cacatua galerita* (Pl. XXVII. fig. 13, *th.g.*), *Calopsittacus*, *Microglossus*, *Chrysotis ochrocephala* (Pl. XXVII. fig. 12, *th.g.*), *Chrysotis æstiva*, *Eclectus pectoralis* (text-fig. 7, p. 231), and *Nestor notabilis* (Pl. XXVII. fig. 22, *th.g.*) the muscle has separated along its whole length from the thyrohyoideus, though still in contact with it, while its free extremity has grown forwards and towards the middle line, and lies in the entoglossal space, well in front of the apex of the thyroid. This stage is thus in advance of the first, in that the muscle has quite separated from the parent one, and in its growth forwards anterior to the apex of the thyroid. *Chrysotis panamensis* belongs to this stage, but the muscle (Pl. XXVII. fig. 14, *th.g.*) at its free extremity is connected with a twig of the sternohyoideus and is confluent with the extremity of its fellow of the other side. This latter condition, or one in which the free extremities of the muscle of either side are in contact, is present in all the Parrots belonging to this stage. But the connection with the sternohyoideus is peculiar, and it is to be noted that the latter is retrogressing—only its fascia remains—at its junction with the thyroglossus. In the absence of a better explanation, we may regard it as an illustration of the tendency to retain old associations, and may assume that in the primitive condition of the muscle,

when as an incorporate part of the thyrohyoideus it arose from the apex of the parahyal process, opposite to the insertion of the sterno-hyoideus, the extremities of the two muscles were more or less confluent, as they are actually in *Conurus holochlorus* (*infra*, p. 240); when the thyroglossus began to separate from the thyrohyoideus and to give up its origin at the parahyal process, it is probable that it carried forward with it a portion of the sternohyoideus.

Chrysotis viridigena stands on the borderland between stages 2 and 3. The muscle is similar to that in *Chrysotis ochrocephala*, but its free extremity is connected to the middle part of the inner surface of the entoglossum, not by tendon or a prolongation of its own substance, but by a definite tract of connective tissue; this tract foreshadows the actual growth forwards of the muscle itself to the entoglossum, such as has occurred in stage 3.

Method B.

Stage 1.

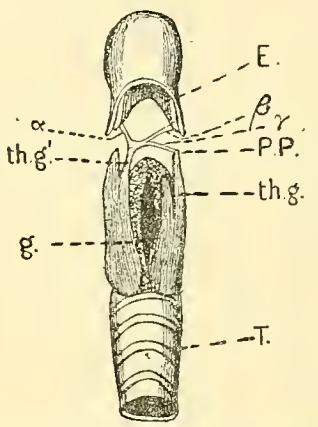
Coracopsis vasa is the sole representative of this stage by this method. The thyroglossus (Pl. XXVII. fig. 17, *th.g.*) is separated from the thyrohyoideus along its whole length; but the course of the two muscles is coincident, their origins and insertions are almost the same. An earlier stage, *i. e.* one in which the thyroglossus is more or less confluent with the thyrohyoideus (only partially separated from it), is not represented in this method. But in view of the mode of origin of the muscle by Method A, and of the intimate relations of the two muscles here, we are justified in the assumption that the thyroglossus of *Coracopsis* has arisen in the same way, by becoming split off from the thyrohyoideus. But in this instance the separation of the two muscles has been completed, and yet the old origin at the parahyal process is retained.

Stage 2.

In *Stringops* (Pl. XXVII. fig. 18) the muscle is similar in its relations to the thyrohyoideus to that in *Coracopsis*, but it gives off a very small twig (*th.g*^{1}.) from its inner side, which is confluent at its extremity with a forwardly directed twig of the stylohyoideus and with the extremity of its fellow of the other side. *Stringops* thus exhibits the first beginning of stage 2, *i. e.* the gradual rejection of its primitive origin *after* the splitting off of the muscle from the thyrohyoideus. The connection of the twig with the sternohyoideus is probably accidental and due to the same cause as the somewhat similar arrangement in *Chrysotis panamensis* (*ante*, p. 235). In *Psittacus* (Pl. XXVII. figs. 15 & 16) the muscle is like that in *Stringops*, but the internal twig (*th.g*^{1}.) is much larger and nearly as large as the body of the muscle, and there is no connection with the stylohyoideus; thus its recession from the primitive origin has progressed to a

greater extent. In *Calyptorhynchus funereus* (probably also in *C. banksii*, where the muscle was injured before the tongue came into my possession), *Cacatua alba*, *Cacatua triton*, and *Nasiterna* the muscle is similar to that in *Psittacus*. In *Nasiterna*, however, the twig (*th.g*^{1}.) does not become confluent with its fellow of the other side, but lies, with no definite attachment in the entoglossal cavity, just beneath the membrane of the tongue. In *Cacatua triton* the twig of either side also branches at its extremity, which thus becomes bifid; this condition foreshadows the peculiar one seen in *Pœocephalus rüppelli* and *Ptistes* (Plate XXVI. figs. 6 & 10). In *Cacatua sulphurea* (text-fig. 8) the twig is continuous with a trifurcate tendinous structure, one

Text-fig. 8.



Cacatua sulphurea.—Dorsal view of thyroglossus. Semi-diagrammatic. (Nat. size.)

E. = entoglossum.
T. = trachea.
P.P. = apex of parahyal process.
th.g. = larger outer branch of thyroglossus.
th g^1. = smaller inner branch of thyroglossus, which on the right-hand side was injured in dissection.
α, β, γ = tendinous branches of *th.g*^{1}.
g. = glottis.

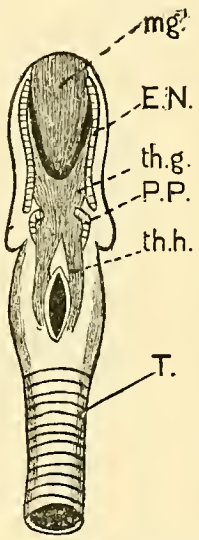
prong (α) of which is attached to the entoglossal of the same side of the tongue, one (β) to the entoglossal of the other side, and the other (γ) to the parahyal process of the other side. Doubtless there is a similar arrangement for the muscle of the other side, but it was unfortunately injured in dissection. To some extent this condition is similar to that in *Pœocephalus* and *Ptistes*; but I prefer to place it in this stage rather than with either of them, because the aforesaid tendinous prolongation of the muscular twig is not such a definite structure as that which apparently represents it in them, and may probably be an individual variation.

Method C.

Stage 1.

In *Brotogerys pyrrhopterus* (text-fig. 9) there is but a single muscle to represent both the thyroglossus and thyrohyoideus. It has a double origin, in part from the inner surface of the posterior half of the entoglossum (E.N.) (= origin of thyroglossus in certain other Parrots) and in part from the inturned apical portion of the parahyal

Text-fig. 9.



Brotogerys pyrrhopterus.—Dorsal view of thyrohyoideus. (Twice nat. size.)

E.N. = entoglossum.
P.P. = parahyal process.
th.h. = thyrohyoideus.
mg'. = tissue identified as mesoglossus.
T. = trachea.
th.g. = the forward prolongation of *th.h.*, and which in other Parrots becomes separated as the thyroglossus.

process (P.P.) (= origin of thyrohyoideus in all Parrots). Its insertion is upon the dorso-lateral surface of the thyroid. The muscle of either side is confluent with its fellow in the middle line in front of the glottis.

In *Conurus cactorum* the condition of the muscle is similar to that in *Brotogerys*, except that the insertion extends ventrally on to the ventro-lateral surface of the thyroid; the representation of the muscle for *Conurus jendaya* (Pl. XXVI. fig. 9) would do for *C. cactorum* if the plane of division there indicated between the thyroglossus and thyrohyoideus were not present.

Stage 2.

In *Pyrrhura leucotis* (Pl. XXVII. fig. 19, *th.g.*) the muscle is similar to that in *Conurus cactorum*; but there is an incipient plane of division existing between that part of the muscle arising from the parahyal process (= thyrohyoideus) and that part arising from the tendon of the hypoglossus obliquus immediately behind the posterior extremity of the entoglossum (= rudimentary thyroglossus). In *Cyanolyseus patagonicus* and *Conurus jendaya* (Pl. XXVI. fig. 9) this incipient division extends backwards, in the latter Parrot almost to the posterior end of the muscle, so that there is now formed a definite and independent thyroglossus, having a separate origin of its own, but merged at its insertion with the posterior part of the thyrohyoideus. The extent of the division in *Cyanolyseus* is intermediate between that in *Conurus jendaya* and *C. cactorum*.

Thus this method is characterized by the fact that the parent muscle (thyrohyoideus) first grows forwards beyond its origin on the parahyal process and forms a second one at the entoglossum (*Brotogerys* and *C. cactorum*); then an incipient plane of division arises anteriorly, which lies between the part of the muscle arising from one origin and that from another (*Pyrrhura*); and, finally, this plane of division becomes more perfect, almost dividing the parent muscle into two independent parts (*Conurus jendaya* and *Cyanolyseus*). The next stage would be that in which the division is complete and would result in the formation of two independent muscles, producing a condition concerning which it would not be possible to say whether it had arisen by one method or the other. Such a condition we will now consider.

The Convergence of Methods A, B, C.

Stage 3.

The result of the evolution of the thyroglossus by either Method A or B is to produce a muscle which has wholly or in part lost its origin, and whose free extremity lies in or near the middle line in front of the thyroid; *Chrysotis viridigena* (*ante*, p. 236) in Method A foreshadows the further evolution of the muscle, and indicates that the entoglossum is destined to constitute the new origin. In Method B there is nothing to definitely indicate the future origin of the muscle which is withdrawing from the old one, but the *à priori* probability is that it will be the same as in Methods A and C. In Method C the entoglossal origin is reached at once before the definite formation of the muscle that is to arise from it has taken place. In all three Methods two stages in the evolution of the muscle may be discerned, and the third stage (that now to be described) is common to all.

The characters that distinguish this stage are: the entoglossal origin and the complete separation of the thyroglossus from the parent muscle (thyrohyoideus). The entoglossal origin is common to this stage and the two stages in Method C, but they

are distinguished in the *complete* separation of the two muscles in the stage now under consideration.

In *Palæornis torquata* (Pl. XXVI. fig. 7, *th.g.*) and *Tanygnathus mülleri* the muscle arises from the inner surface of the entoglossum a little anterior to its posterior extremity, and is inserted at the dorso-lateral surface of the thyroid; it is narrow at its origin, but very wide at its insertion. In *Loriculus galgulus* (Pl. XXVII. fig. 23) the muscle is like that in *Palæornis*, but it arises from the posterior extremity of the entoglossum. In *Ara ararauna* the muscle is similar to that in *Palæornis*, but it is much attenuated. In *Ara macao* (Pl. XXVII. fig. 20) the muscle is well developed and arises from the tendon of the hypoglossus obliquus just posterior to the origin of the latter from the posterior extremity of the entoglossum; its insertion is for the most part to that portion of the membrane (*m.*) of the tongue that covers the thyroid on either side of the glottis, and also to a small extent to the upper margin of the dorso-lateral surface of the thyroid. In *Pionopsittacus pileatus* the muscle resembles that in *Palæornis*, but its origin is tendinous. In *Psittinus incertus* the muscle appears to be double. It consists of two perfectly distinct parts closely bound together by connective tissue, which arise from the posterior extremity of the entoglossum, and become inserted, one to the dorso-lateral surface, and the other to the ventro-lateral surface of the thyroid. The former of these parts is undoubtedly a thyroglossus, and the latter, in virtue of its insertion, is a thyrohyoideus, but a thyroglossus on account of its origin: probably it is a thyrohyoideus that has acquired a new origin, and we can understand how, if old associations tend to be preserved and the thyroglossus arose by *Method C*, that it was carried forward to the entoglossum.

In *Ptistes erythropterus* (Pl. XXVI. fig. 6) the condition that is foreshadowed in *Cacatua triton* (*ante*, p. 237) has attained its full development, for the rudimentary bifid nature of the free extremity of the muscle there indicated has in *Ptistes* developed into a well-pronounced fork of two prongs, the larger of which has formed a tendinous origin at the inner surface of the posterior lateral process of the entoglossal of the same side of the tongue, while the smaller one crosses the middle line and reaches its origin at the same position on the entoglossal of the other side.

Stage 4.

In this stage the muscle is characterized by having a double origin, *i. e.* one from the entoglossum and another, more or less strongly developed, from the parahyal process.

In *Deroptyus accipitrinus* that part of the muscle which arises from the entoglossum is very much the stronger of the two, and in fact constitutes almost the whole of the origin; the part arising from the parahyal process consists of only a few fibres. The insertion is the usual one. In *Conurus holochlorus* the two origins are more nearly equal, that at the entoglossum being slightly larger than the other; the part arising

from the parahyal process is confluent with the tendon of the stylohyoideus at its insertion on the apex of the parahyal process.

In *Pœocephalus rüppelli* (Pl. XXVI. fig. 10) the entoglossal portion (*th.g*^{1}.) of the muscle is split into two branches, and is similar to that described for *Ptistes* (*ante*, p. 240). Of the two branches, the smaller one takes its origin from the entoglossal of the same side, while the much larger one passes over to the entoglossal of the other side, and arises from this at its posterior extremity by an origin common to it and the smaller branch of the muscle of the other side. Thus the muscle at its origin from the entoglossal of either side consists of two sets of fibres : of a larger set derived from the muscle of the other side and a smaller set derived from the muscle of the same side; the fibres of the two muscles are thus distributed and cross each other in precisely the same way that the nerve-fibres of the optic tract of mammals do. The parahyal portion (*th.g.*) of the muscle is smaller than the combined entoglossal portion. In *P. robustus* there is the same general arrangement and optic-chiasma-like condition of the muscle ; but the parahyal portion is larger than the entoglossal, and the larger branch of the entoglossal part belongs to the same side and the smaller to the other side, which is just the reverse to that in *P. rüppelli*.

The condition which the muscle exhibits at this stage (Stage 4) may be interpreted in two ways: either the parahyal portion is retaining, to a greater or less extent, its primitive relation to the parahyal process, or, it is secondarily coming back to it after it had attained a wholly entoglossal origin. It is necessary to decide, as far as possible, which of these two alternatives is the more probable ; and since the answer depends upon the condition of the muscle in the later stages of its evolution, I shall proceed first to their description.

Stage 5.

The relations of this muscle at this stage are somewhat similar to Stage 1 in Method B. It arises from the apex of the parahyal process, and is inserted into the dorso-lateral surface of the thyroid. It thus corresponds in its origin, and nearly so in its insertion, to that in *Coracopsis*, which I have placed at a much earlier stage; but there is a difference—which, however, does not hold true in all cases—in that at this stage the insertion of the thyrohyoideus is distinctly ventrad of the thyroglossus, whereas in *Coracopsis* the two muscles run an almost coincident course, not only at their insertion, but along their whole length. The further reasons that have induced me to consider similar conditions as belonging to two distinct stages I shall mention later (*infra*, p. 243).

Platycercus eximius (Pl. XXVI. fig. 11, *th.g.*) may be taken as typical of this stage; the thyroglossus arises from the apical region of the parahyal process dorsad of that of the thyrohyoideus, and retains this position with respect to the latter muscle along its whole course, including its insertion. If it be compared with that of *Coracopsis* (Pl. XXVII. fig. 17) the difference in its relation to the thyrohyoideus is apparent, for

in *Platycercus* it is situated dorsally and in *Coracopsis* laterally to that muscle. In *Psephotus xanthorrhous*, *Nymphicus uvæensis*, *Caica leucogaster*, *Prioniturus* sp.?, *Cyanorhamphus auriceps*, *Pyrrhulopsis splendens* and *P. personata*, *Psittacula passerina*, and *Pezoporus formosus* (Pl. XXVI. fig. 8) the muscle is similar to that in *Platycercus*. In *Bolborhynchus lineolatus* the muscle is similar to that in *Platycercus*, but it is confluent at its origin, and along its ventral border at its insertion, with the thyrohyoideus; along the remainder of its course it is free of that.

Stage 6.

In this stage the muscle arises from the hypocleidium (apex) of the completed parahyal arch, and is inserted into the dorso-lateral surface of the thyroid (Pls. XXVII. & XXIX. figs. 21 & 50). It thus differs in respect of its origin from that in Stage 5, in that it arises from the median projecting process formed by the union of the parahyal crura (*cf.* Mivart, P. Z. S. 6 & 7), instead of from the parahyal processes. Although the muscle (Pl. XXIX. fig. 50) lies dorsally to the thyrohyoideus along the major portion of its course, the latter muscle at its insertion turns upwards and, passing between the thyroglossus and the thyroid, becomes inserted into the dorso-lateral surface of the latter. In *Eos riciniata* the thyroglossus is merged with the thyrohyoideus at its origin, but otherwise is similar to that in *Lorius*. In *Vini australis* the muscle is confluent with the thyrohyoideus both at its origin and insertion. The confluence of the two muscles in these two genera at these particular parts must not be regarded as indicating a primitive condition, for it is probable that this confluence is secondary, and arises from the fact that in these areæ the two muscles are in contact.

A survey of the variations presented by this muscle thus substantiates the statement made (*ante*, p. 235) that it started along the road of its evolution from three initial stages, all of which ultimately lead to a common stage, the third stage in the evolution of the muscle. *Cacatua roseicapilla* and *C. leadbeateri* belong to one of these initial stages, *Coracopsis* to another, and *Brotogerys* and *Conurus cactorum* to the other. Each of these initial stages passes along its own line of development to a second, and each of these converges to a third stage, which is similar in all. This latter stage is characterized by the entoglossal origin of the muscle, and it appears to be, like those that preceded it, but a temporary one, for the muscle, having left the parahyal process to extend to the entoglossum, begins to return to its primitive origin. The first step in that return is indicated in *Deroptyus accipitrinus*, where the origin of the muscle is double; the greater part arises from the entoglossum, but a few fibres, however, take their origin from the parahyal process. I interpret the parahyal origin as representing the first return of a few fibres back from the entoglossal origin. In *Conurus holochlorus* a greater number of fibres have returned, and the two origins are nearly equisized. The condition of the muscle in *Pœocephalus* is fundamentally the same, but its entoglossal portion has specialized in its own direction. From this

stage, which constitutes the fourth one, to the next is somewhat sudden, since in Stage 5 the whole of the remaining portion of the muscle has returned to the parahyal process. In the final stage, owing to the formation of a completed parahyal arch, by the growth forwards and meeting in the middle line of the parahyal processes, with the formation of a median symphysis, the hypocleidium, the muscle arises not from the crura, but from the hypocleidium.

It may be objected that the interpretation of the facts represented in Stage 4 implies that the origin from the parahyal process is at once the most specialized and the most primitive condition. Such an objection would be quite valid were it not that other facts in the lingual myology support the conclusion arrived at by the consideration of those relating to the thyroglossus; and, moreover, there is a difference between the two stages with respect to the insertion and the general course of the muscle in relation to the thyrohyoideus (*cf. ante*, p. 241). If we arrange in two columns those Parrots in which the thyroglossus arises from the parahyal process—in one column those which my interpretation of the facts lead me to regard as primitive, and in the other those which I regard as specialized—the divison will be as follows:—

I. Primitive.	II. Specialized.
Wholly from the parahyal process. — *Coracopsis.*	*Eos.*
In part only from the parahyal process. — *Psittacus.*	*Vini.*
Stringops.	*Lorius.*
Cacatua alba.	*Caica.*
„ *triton.*	*Cyanorhamphus.*
Nasiterna.	*Nymphicus.*
Calyptorhynchus.	*Platycercus* and some other members of Stage 6.

Now a glance at the table of characters (pp. 266–269) of the inferior ceratoglossus will show that those Parrots in which I regard the parahyal process origin of the thyroglossus as secondary (column II.), and as distinct from those in which I regard it as primitive (column I.), are, in virtue of the characters of that muscle, very much specialized: some of them, in respect of the tendon and the amount of retrogression of the ceratoglossus inferior anticus, are more advanced than others, but all of them have reached their fullest development with regard to the extension posteriorly along the hypobranchial of the ceratoglossus inferior posticus. It is very different, however, with the inferior ceratoglossus of those Parrots arranged in column I.: four of the

seven belong to the most primitive stages, and the other two are not very much more advanced. And it is interesting to note that *Deroptyus* and *Conurus holochlorus*, although placed with *Psittacus* and *Coracopsis* in respect of the character of the inferior ceratoglossal tendon, are intermediate between them and the members of column II. in the remaining characters of that muscle, which is a position they should occupy if my interpretation of the nature of the parahyal fibres of their thyroglossus muscle is correct. In *Pœocephalus*, the thyroglossus of which, according to the meaning here attached to it, is the most advanced of Stage 4, the characters of the inferior ceratoglossal are identical with those of some of the Parrots in column II.

To state the facts in a briefer form, we may say that there are two sets of Parrots with a parahyal process origin for the thyroglossus. In one of these sets the ceratoglossus inferior is primitive and in the other specialized. Hence has arisen the conclusion that the parahyal process origin in the one case is primitive and in the other secondary. And, seeking for a logical demonstration of the truth of this conclusion, we must find a Parrot which in respect of its ceratoglossus inferior must be intermediate between the two sets of Parrots, and in the characters of its thyroglossus must show the transition from the entoglossal origin—which has been traced from the primitive parahyal process stage—to the secondary parahyal process stage: such Parrots are *Deroptyus*, *Conurus holochlorus*, and *Pœocephalus*; and they exhibit, as far as the first half of the gap, a graded series.

The conclusion is further corroborated by a consideration of the amount of extension of the hypoglossus obliquus. In those Parrots in which I regard the thyroglossus origin at the parahyal process as being primitive, the hypoglossus obliquus is limited to the head of the hypobranchial, and in two instances only extends back along that through the anterior third; but in those in which the parahyal process origin is secondary the hypoglossus obliquus extends backwards along the whole length of the hypobranchial in the majority of instances, and in only a few as far as the anterior two-thirds.

If the conclusion that the parahyal process origin of Stages 5 and 6 of the thyroglossus is not accepted, the only other alternative is to believe that this muscle has remained primitive in Parrots in which other muscles have advanced to a specialized condition, and that it has advanced to more or less specialized conditions in Parrots in which other muscles have remained primitive or have advanced but slightly.

The evolution of the muscle is graphically represented in the following Table:—

The Evolution of the Thyroglossus, graphically represented.

Thyrohyoideus.

C

Thyroglossus arises as a direct forward prolongation of thyrohyoideus to the entoglossum.

Stage 1.

Brotogerys. *Conurus cactorum.*

Stage 2.

A plane of partial division separates the thyroglossus from thyrohyoideus.

Pyrrhura. *Cyanolyseus.*

A

Thyroglossus branches off at once from thyrohyoideus.

Stage 1.

The free extremity of thyroglossus does not lie in front of thyroid.

Cacatua roseicapilla. *Cacatua leadbeateri.*

Stage 2.

Extremity of thyroglossus lies well in front of thyroid.

Cacatua galerita.
Calopsittacus.
Microglossus.
Chrysotis ochrocephala.
Chrysotis æstiva.
„ *panamensis.*
Eclectus.
Nestor.

B

Thyroglossus separates from thyrohyoideus gradually *after* a plane of division has formed.

Stage 1.

The thyroglossus still retains its primitive origin at parahyal process.

Coracopsis.

Stage 2.

The thyroglossus is beginning to withdraw from the parahyal process.

Psittaeus. *Calyptorhynchus.* *Cacatua triton.*
Stringops. *Cacatua alba.* *Nasiterna.*

Stage 3.

Thyroglossus arises from the entoglossum, and is completely, or almost completely, separated from the thyrohyoideus.

Chrysotis viridigena. *Tanygnathus.* *Pionopsittacus.*
Ara macao. *Conurus jendaya.* *Loriculus.*
„ *ararauna.* *Psittinus.* *Ptistes.*

Stage 4.

Thyroglossus arises in part from entoglossum and in part from parahyal process.

Deroptyus. *Pœocephalus rüppelli.*
Conurus holochlorus. „ *robustus.*

Stage 5.

Thyroglossus arises from parahyal process.

Prioniturus. *Pezoporus.* *Cyanorhamphus.*
Bolborhynchus. *Pyrrhulopsis.* *Psittacula.*
Platycercus. *Nymphicus.* *Caica.*

Stage 6.

Thyroglossus arises from hypocleidium.

Lorius domicella. *Eos riciniata.*
„ *flavo-palliatus.* *Vini australis.*

The Hypoglossus Muscle.

(*a*) *Hypoglossus obliquus*.—The variations exhibited by this muscle may be considered under three heads: 1st, the amount of its extension backwards upon the hypobranchial; 2nd, the degree of development of its tendon or tendinous fascia; 3rd, its divided or undivided condition. The advance of an individual muscle in respect of any one of these characters is not always accompanied with a corresponding advance of the other two; but if the muscles are arranged in sets, each set representing a stage in the progression of one of these three characters, it will be found that the majority in each set are advanced in respect of the other two characters.

The muscle arises in part from the hypobranchial and in part from the ventral and dorsal surfaces of the body of the basihyal, and is inserted into the inner surface and posterior margin of the *posterior lateral process* of the entoglossum. In some Parrots (Pls. XXVIII. & XXIX. figs. 29 & 48) (*cf.* pp. 266–269) the muscle (*hg.o.*) is divided into two in a longitudinal direction, in such a way that an outer portion related to the hypobranchial is separated from an inner one related to the basihyal, both retaining the origin insertion. But in *Lorius* the plane of division does not thus divide the muscle, for the outer portion is related both to the hypobranchial and basihyal (Pl. XXIX. fig. 37).

Stage 1.

The most primitive condition of the muscle is that in which its origin is almost wholly confined to the basihyal, and posteriorly does not extend farther than to the anterior head of the hypobranchial; it is further generally characterized by the absence of a tendon or tendinous fascia and by the fact that it is not divided into two portions. (*Cf.* the table of characters of *Hypoglossus obliquus*, pp. 266–269.)

Stage 2.

In this stage the muscle has extended backwards as far as the anterior third or half of the hypobranchial. The fascia is usually tendinous or a weak tendon is developed; but in some few instances (*Nestor*) a strong tendon is present. The muscle is divided in about 50 per cent. of the Parrots.

Stage 3.

The muscle extends to the anterior two-thirds of the hypobranchial, and in most instances the tendon is fairly strongly developed, and in a few strongly; in one (*Deroptyus*) it is absent, and neither is the fascia tendinous. The muscle is divided in all except three.

Stage 4.

This is the final stage, and it is marked by the extension of the muscle to the posterior extremity of the hypobranchial; in all instances the tendon is strongly developed, and in a few instances very strongly so. The muscle is divided in all, with but two exceptions.

(β) *Hypoglossus rectus.*—This muscle (*hg.r.*) arises from the outer surface of the *posterior lateral process* of the entoglossum and is inserted tendinous partly into the apex of the tongue and partly into the fascia of the mesoglossus (Pl. XXIX. fig. 50). It exhibits but very little variation, and such as it does consists in the length and breadth of its insertion tendon and in the single or paired condition of that. In the majority of Parrots the tendon of each half of the muscle is confluent with its fellow of the other side; but in a few (*Lorius, Eos, Ara ararauna*) it is double. In *Lorius domicella* the tendon is narrow but thick, and tends to be cylindrical in form. It appears to be a muscle that works in conjunction with the mesoglossus, partly in the working of the "brush" of the tongue in the Lories and *Nestor*, and partly in depressing the apex of the tongue in all. The tendon of the muscle moves over the rounded cartilaginous extremity of the entoglossum.

In *Nestor* (Pl. XXIX. fig. 46) both the muscle and its tendon are very long, a condition which is correlated with the great length of the entoglossum. In *Stringops* (Pl. XXVIII. fig. 26), as in a few others, it is muscular up to its insertion, but the fascia is quite tendinous in the middle of its length.

Mylohyoideus Muscle.

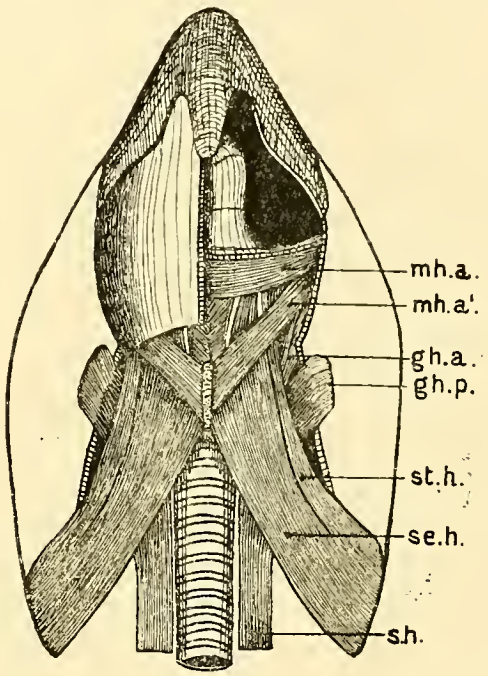
(*a*) *Mylohyoideus anterior.*—This muscle consists of two parts—a usually wider, more superficial anterior (Pl. XXVI. fig. 5, *mh.a.*) and a deeper posterior portion (*mh.a*^{1}.). The two parts arise from a common origin at the antero-dorsal corner of the rami of the lower jaw (text-fig. 10, p. 248), just behind the line that marks the posterior limit of the bill (*b.*). The two halves of each portion unite with each other in the middle line, in some instances becoming confluent, but in others uniting in a tendinous tract at their junction. The anterior portion is never, in any way, attached to the hyoid bone, and simply passes across the inter-ramal area, ventrad of the hyoid; between its median part and the body of the basihyal there lies a glandular organ of tough consistency which opens to the buccal cavity by paired lateral ducts, and, in addition to any glandular function which it may perform, serves to bring the muscle into mechanical connection with the hyoid. The posterior portion (text-fig. 15, p. 260) is usually inserted into a bony or cartilaginous nodule (N.) which articulates with the ventral surface of the urohyal, and to which it is closely bound by a sheath of connective tissue; quite exceptionally it may be inserted into the basihyal just at the origin of the urohyal.

In contrast to the condition existing (4) among the *Ratites, Raptores,* and *Penguins,* the muscle, with one exception, is confined to the anterior third and less of the inter-ramal area, and in many exhibits evident signs of retrogression. In a few instances the anterior and posterior parts are about equally strongly developed, but in the majority the latter is less well developed than the former, and in some has almost disappeared. The anterior portion in a large number of Parrots exhibits evidence that it was primitively more extensive in a posterior direction. In some cases the lower jaw is backwardly extended, and the two portions of the muscle are then completely

hidden; in others the anterior part only is covered, and in yet others neither portion is covered.

Undoubtedly the most primitive condition of the muscle is that exhibited in *Stringops* (Pl. XXVI. fig. 2, *mh.a.*), where it extends backwards to the posterior portion of the inter-ramal area. Anteriorly, it arises in the way already indicated, but posteriorly it arises on either side in the form of a narrow crescentic band of

Text-fig. 10.



Conurus jendaya.—Ventral view. On the left, half of the mandible has been removed, but otherwise the parts are *in situ*. (Twice nat. size.)

Additional letters.

gh.a. = geniohyoideus anterior.
gh.p. = „ posterior.
mh.a. = mylohyoideus anterior.
mh.a'. = „ „ (posterior portion).
s.h. = sternohyoideus.
se.h. = serpihyoideus.
st.h. = stylohyoideus.

muscular tissue, from the same origin as the serpihyoideus. It has undergone considerable retrogression, for the whole of its middle third consists of nothing but the persistent fascia of the muscle, and even in the middle line of the anterior third the muscular fibre has disappeared. The posterior portion (*mh.a'.*) lies in the same position that it occupies in other Parrots, but it is inserted to the connective-tissue sheath that invests the urohyal, a cartilaginous nodule not being present.

In *Loriculus* (Pl. XXIX. fig. 51), *Pionopsittacus*, *Coracopsis*, *Cyanolyseus*, *Eclectus*, *Nestor*, *Cacatua roseicapilla*, *Bolborhynchus*, and *Pœocephalus robustus* the anterior portion of the muscle has undergone still greater retrogression, and is only represented by a muscular band occupying the anterior fifth or slightly more of the inter-ramal space; from the posterior border of the muscle (Pl. XXIX. fig. 51, *f.*) a connective-tissue sheath continuous with its fascia extends backwards to about the posterior end of the rami.

In *Psittacus* (Pl. XXVI. fig. 3), *Pyrrhura*, *Psittinus*, and *Cacatua* (Pl. XXVI. fig. 4) the muscle is similar to that just described, but the persistent fascia (*f.*) is not so large, and consists of a tract extending from the muscle for a short distance only, with a lateral strip running back along the outer border of the stylohyoideus. In *Psittacula* and *Caica* the lateral strips are absent. In *Cacatua* there is a similar persistent portion of the fascia (*f.p.*) to the posterior part of the muscle, which extends backwards; and in *C. leadbeateri* there is in addition an anteriorly extended fascia devoid of muscle-fibre.

In *Chrysotis*, *Tanygnathus*, *Ptistes*, *Vini*, and *Lorius* (text-fig. 12, p. 251) the anterior portion of the muscle is restricted to the anterior fifth or less of the inter-ramal space, and the persistent fascia is reduced to a pair of lateral strips, which in *Chrysotis ochrocephala* are very small. In the remaining Parrots the muscle is restricted to the anterior third or less of the inter-ramal area, and there is no representative of the persistent fascia.

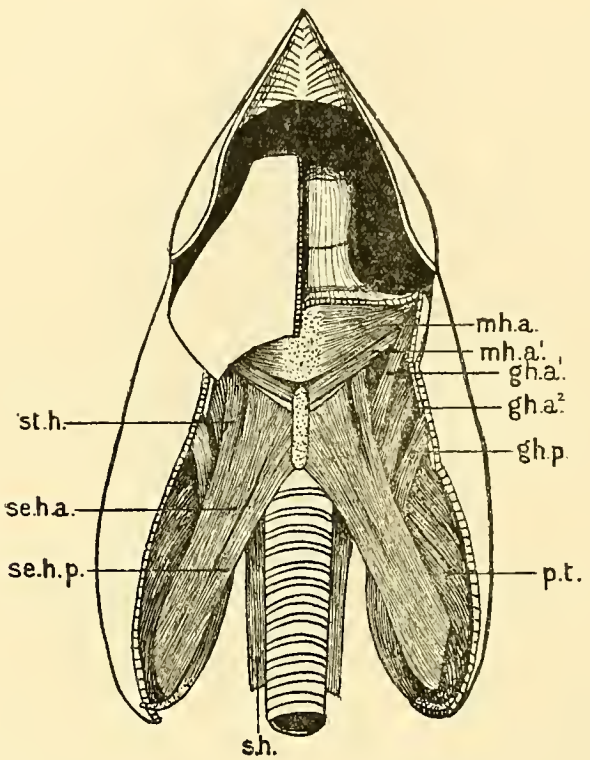
In *Cacatua* (Pl. XXVI. fig. 4), *Calopsittacus novæ-hollandiæ*, *Cyanolyseus*, *Chrysotis*, *Conurus* (text-fig. 10), *Psittacus* (Pl. XXVI. fig. 3), *Pœocephalus*, *Pyrrhura*, *Coracopsis*, *Vini*, *Lorius*, and *Eos* the posterior portion of the muscle is as strongly, or nearly as strongly, developed as the anterior. In *Prioniturus*, *Psephotus*, *Platycercus*, *Calyptorhynchus*, *Cyanorhamphus*, *Ptistes*, *Psittacula*, *Psittinus*, *Eclectus*, *Tanygnathus*, *Pezoporus*, *Pyrrhulopsis*, *Nasiterna*, *Loriculus*, *Bolborhynchus*, *Pionopsittacus*, *Palæornis* (text-fig. 11), and *Brotogerys* (text-fig. 13, p. 252) the posterior portion is smaller than the anterior; in the last two Parrots it is very small, and in *Brotogerys* and *Caica* has almost undergone complete retrogression, being represented by a few fibres only. In *Microglossus* and *Nestor* the posterior portion is absent, the probable meaning of which is that it has disappeared.

In *Microglossus*, *Cyanolyseus*, *Ara* (text-fig. 15, p. 260), *Caica*, *Pœocephalus*, and *Pyrrhura* both the anterior and posterior portions of the muscle are hidden by the lower bill; in *Eos*, *Conurus*, *Psittacula*, *Tanygnathus*, and *Nasiterna* the anterior portion alone is completely hidden; in *Palæornis* (text-fig. 11), *Ptistes*, *Platycercus*, *Pezoporus*, *Prioniturus*, *Psephotus*, and *Cyanorhamphus* the anterior half only of the anterior portion is thus hidden; and in *Cacatua* (Pl. XXVI. fig. 4) the anterior third only. In *Brotogerys*, *Loriculus*, *Pionopsittacus*, *Psittacus* (Pl. XXVI. fig. 3),

Calopsittacus, *Eclectus*, *Chrysotis*, *Psittinus*, *Nestor*, and *Lorius* neither portion is covered by the mandible. I was able to obtain the tongues only of *Pyrrhulopsis* and *Calyptorhynchus*, and could not, therefore, examine the particular feature now considered.

In the great majority of Parrots the halves of the posterior portion of the muscle are inserted one on either side to a bony or cartilaginous nodule (N.) that lies at the anterior end of the urohyal upon its ventral surface, and to which it is fastened by a

Text-figure 11.



Palæornis torquata.—Ventral view. On the left, one-half of the lower bill has been removed, and the rami of the mandible slightly pulled outwards to show the origin of the geniohyoideus (*gh.a*¹., *gh.a*²., and *gh.p.*). (Twice nat. size.)

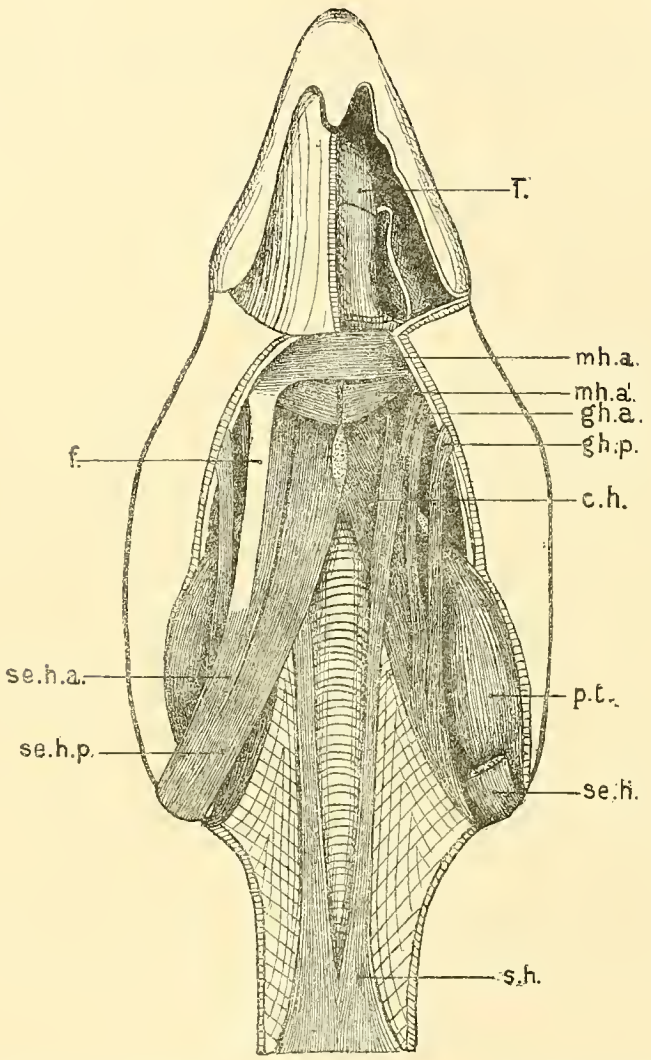
Additional letters.

*gh.a*¹. & *a*². = anterior and posterior branches of anterior division of geniohyoideus.
se.h.a. = serpihyoideus anterior.
se.h.p. = serpihyoideus posterior.
s.h. = sternohyoideus.
p.t. = pterygoideus.

sheath of connective tissue. In *Chrysotis* this nodule is absent, and the muscle is inserted directly to the sheath investing the urohyal at the root of that. In *Conurus* (text-fig. 10) (*C. holochlorus* excepted) the nodule is elongated and extends to the posterior extremity of the urohyal, the insertion of the muscle following the extension of the nodule; *Calyptorhynchus* is similar in respect of that. In *Eclectus* it is inserted to the cartilaginous continuation of the urohyal.

In *Palæornis* (text-fig. 11), *Ptistes*, *Psittacus*, *Ara*, *Pœocephalus*, *Calopsittacus*, *Pezoporus*, *Nasiterna*, *Prioniturus*, *Platycercus*, *Psephotus*, *Cyanorhamphus*, and

Text-figure 12.



Lorius domicella.—Ventral view. On the left the serpihyoideus (*se.h.a.* and *se.h.p.*) has been removed to show the ceratohyoideus (*c.h.*), the sternohyoideus (*s.h.*), and the geniohyoideus (*gh.a.* and *gh.p.*). (Twice nat. size.)

Additional letters.

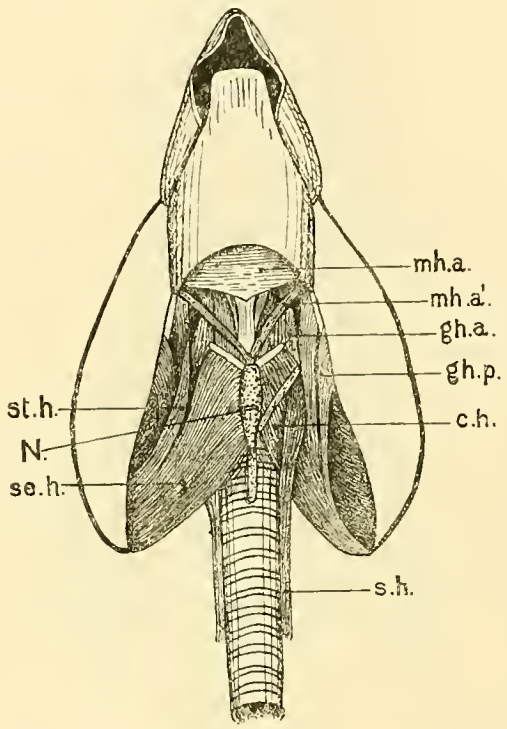
c.h. = ceratohyoideus.	*p.t.* = pterygoid muscle.
f. = fascia.	*t.* = tongue.

Lorius domicella (text-fig. 12, p. 251) the posterior portion lies immediately behind the anterior one, in such a way that the anterior margin of the former is almost in

contact with the posterior margin of the latter. In *Eclectus*, *Pyrrhura*, *Psittinus*, and *Lorius flavo-palliatus* (text-fig. 14, p. 256) the interval is a little greater. In *Eos*, *Chrysotis*, *Conurus* (text-fig. 10, p. 248), *Cyanolyseus*, and *Brotogerys* (text-fig. 13, p. 252) the interval is very great, except of course at the common origin of the two portions.

The general conclusion arising from the foregoing facts is that both the anterior and posterior portions of the muscle are undergoing retrogression. *Stringops* stands alone

Text-figure 13.



Brotogerys pyrrhopterus.—Ventral view. On the left the serpihyoideus has been partially cut away. (Twice nat. size.)

Additional letter.

N. = cartilaginous nodule.

in that its muscle exhibits the most primitive condition, all the others in respect of this muscle having attained a fairly advanced progression, some slightly more than others. There is no definite comparison possible in any given individual between the stage of specialization reached by this muscle and that attained by either the ceratoglossus or thyroglossus muscle.

The more or less extensive connective-tissue sheet, or strip, that extends backwards from the muscle in some Parrots is shown to be a persistent fascia in virtue of the facts that it is continuous with the ventral and dorsal fasciæ of the muscle, and that, in

Chrysotis æstiva, there are pigmented blood-capillaries, which, when microscopically examined, show the characteristic meshwork of muscular blood-capillaries; moreover, the condition of the muscle in *Stringops* is such as to leave no room for doubt as to the nature of this tissue.

The retrogression of the posterior portion of the muscle can be traced, step by step, up to its complete disappearance in *Nestor* and *Microglossus*. It is strange that such a generalized tongue as that of the latter Parrot should have reached, in respect of this, the most advanced stage.

(β) *Mylohyoideus posterior*.—This muscle is composed of two portions—an inner, more posterior *serpihyoideus* (*se.h.p.*), and an outer, more anterior *stylohyoideus* (*se.h.a.*). In all Parrots, except the Loriidæ, both portions are present, but in them the stylohyoideus is absent; it will be shown that the Loriidean condition is specialized.

The serpihyoideus and stylohyoideus arise from a common origin at the posterior extremity of the mandible, and passing forwards as a single muscle for a greater or less distance they separate, and the former becomes inserted partly into the nodule lying on the ventral surface of the urohyal, or, in the absence of the nodule, into the sheath investing the urohyal, and partly into the uro-hypobranchial tendon, which is attached at one end to the urohyal nodule (N.) and at the other to the head of the hypobranchial; the stylohyoideus turns outwards, passes round the lateral ceratoglossal, parallel with and in front of the sternohyoideus, and reaches its insertion into the outer lateral surface of the parahyal process.

In *Cacatua* (Pl. XXVI. fig. 4, *se.h.*), *Conurus jendaya*, *C. cactorum*, *Psittacula*, *Cyanolyseus*, *Ptistes*, *Coracopsis*, *Bolborhynchus*, *Loriculus*, and *Brotogerys* (text-fig. 13) the serpihyoideus is a single undivided muscle. In *Cacatua galerita* (Pl. XXVIII. fig. 25) the muscle sends a small tongue-like projection on to the ventral surface of the uro-hypobranchial tendon, which nearly meets the origin of the ceratoglossus inferior anticus accessorius, and another along the outer extremity of the tendon; in *C. roseicapilla* this inner tongue-like projection is much wider. In *Pionopsittacus* the muscle exhibits a remarkable contraction of its substance at its origin, which is tendinous, and foreshadows the condition of that in *Eos* and *Pezoporus*.

In *Conurus holochlorus*, *Eclectus*, *Palæornis* (Pl. XXVIII. fig. 32), and *Pyrrhura* (Pl. XXIX. fig. 40) the serpihyoideus shows a very incipient division of the muscle into an outer and inner portion, in the form of a slight, almost imperceptible thinning of the muscle-fibres in the middle line at the anterior end of the muscle. In *Palæornis* there is in addition a very slight plane of division continued backwards from the thinned area, and more marked in the right than the left muscle.

In *Chrysotis* (Pl. XXVIII. fig. 28), *Cacatua sulphurea*, *Calopsittacus*, *Ara ararauna* (Pl. XXVIII. fig. 24), *Psittacus* (Pl. XXVI. fig. 3), *Nasiterna*, *Caica*, *Calyptorhynchus funereus*, and *Tanygnathus* the thinned area of retrogression is more marked and

muscle-fibres have disappeared from it, leaving only the fascia behind. In *Cacatua sulphurea* the retrogression in the right-hand muscle is more pronounced than in the left. In *Psittinus*, *Lorius domicella* (text-fig. 12), *Cyanorhamphus*, *Prioniturus*, *Platycercus* (Pl. XXVI. fig. 5), and *Calyptorhynchus banksi* the area of retrogression has extended posteriorly and become a definite plane of division, which divides the muscle into two distinct parts along the length of its anterior two-thirds or more. In *Lorius flavo-palliatus* (text-fig. 14) the separation is very distinct, but does not extend beyond the anterior fifth. In *Stringops* the division only extends to the anterior half. In *Pezoporus* (Pl. XXIX. fig. 47) the muscle is divided into two parts along its whole length, and the origin of the inner of the two parts exhibits a remarkable contraction similar to that in *Eos* (Pl. XXVI. fig. 1), but it possesses no tendon or tendinous thickening of the fascia. In *Pœocephalus rüppelli* the plane of division does not quite reach to the posterior extremity of the muscle, but the inner portion exhibits at its origin the peculiar contraction of its substance above mentioned, and in addition it has developed a weak and small tendon; the division of the muscle is not quite so complete on the left as on the right side. In *Pœocephalus robustus* the right-hand muscle is not divided to a greater extent than the left-hand one in *P. rüppelli*, and the left-hand one not at all; otherwise it is as that in *P. rüppelli*. In *Eos* (Pl. XXVI. fig. 1) this condition reaches its maximum development; the muscle is very strongly developed, and divided along its whole length into two portions, of which the inner overlaps the outer one posteriorly, and at its contracted origin has developed a well-marked tendon which extends forwards along the outer margin of the posterior half of the muscle. In *Nestor* (Pl. XXIX. fig. 46, *se.h.*) there appears to be only a single portion present, and this probably represents only the inner portion, since its insertion corresponds to that; that part of the uro-hypobranchial tendon which represents the insertion of the outer part in other Parrots is free and gives no insertion to any muscle. In *Nestor* therefore the outer part has probably quite retrogressed. In *Lorius* (Pl. XXIX. figs. 37 & 38), *Eos*, and *Vini* the uro-hypobranchial tendon (*u.ten.*) has the same relations as that in other Parrots, and the outer portion of the serpihyoideus is inserted to it as in them; but in addition the antero-outer corner of the muscle is prolonged forwards and forms an independent insertion (*ins.*), slightly tendinous, on the basihyal between the lateral and anterior portion of the inferior ceratoglossals.

In *Cacatua* (Pl. XXVIII. fig. 25), *Psittacus* (Pl. XXVI. fig. 3), *Stringops*, *Eclectus*, *Calyptorhynchus*, *Ptistes*, and *Conurus cactorum* the stylohyoideus is confluent with the serpihyoideus along the length of its posterior half. In *Chrysotis* (Pl. XXVIII. fig. 28), *Coracopsis* (Pl. XXVIII. fig. 31), *Conurus jendaya*, *C. holochlorus*, *Psittinus*, *Bolborhynchus*, *Pyrrhura*, *Pezoporus* (Pl. XXIX. fig. 47), *Psittacula*, *Pœocephalus*, *Palæornis*, *Platycercus*, *Nasiterna*, *Loriculus*, *Brotogerys*, *Psephotus*, and *Caica* the two muscles are confluent only at their origin, or for a very little way in front of that.

In *Ara* (Pl. XXVIII. figs. 24 & 27), *Nestor* (Pl. XXIX. fig. 46), and *Pionopsittacus* the two muscles are not confluent at any portion of their course, though they arise side by side from the posterior extremity of the mandible. In *Ara ararauna* the stylohyoideus crosses the ventral surface of the serpihyoideus just after its origin.

In *Palæornis*, *Eclectus* (Pl. XXIX. fig. 49), *Bolborhynchus*, *Psephotus*, *Ara ararauna* (Pl. XXVIII. fig. 24), *Conurus jendaya*, *Cacatua*, and *Chrysotis* the stylohyoideus exhibits a slight retrogression of its muscle-fibres at its origin, the fascia remaining. In *Ara macao* (Pl. XXVIII. fig. 27), *Conurus cactorum*, *Pezoporus* (Pl. XXIX. fig. 47), *Pœocephalus*, *Pionopsittacus*, and *Stringops* (Pl. XXVIII. fig. 26) the retrogression is more considerable, and in *Stringops* and *Pezoporus* it practically involves the whole origin and a considerable portion anteriorly to that. In *Pezoporus* the whole of the left-hand muscle has retrogressed and not a trace of it can be found, while, as already indicated, the origin of the right-hand one has practically disappeared; the insertion has also retrogressed, for it is represented (Pl. XXVI. fig. 8) by a mere filament of connective tissue, and the muscle can be, therefore, of no functional value. In *Nymphicus* the insertion is also reduced to the condition of a mere filament. In *Platycercus* (Pl. XXVI. figs. 5 & 11) also the muscle is very thin and suggestive of an early disappearance. In *Pionopsittacus* (Pl. XXIX. fig. 43) there is the same advanced retrogression, for its origin is gone and its insertion nearly so.

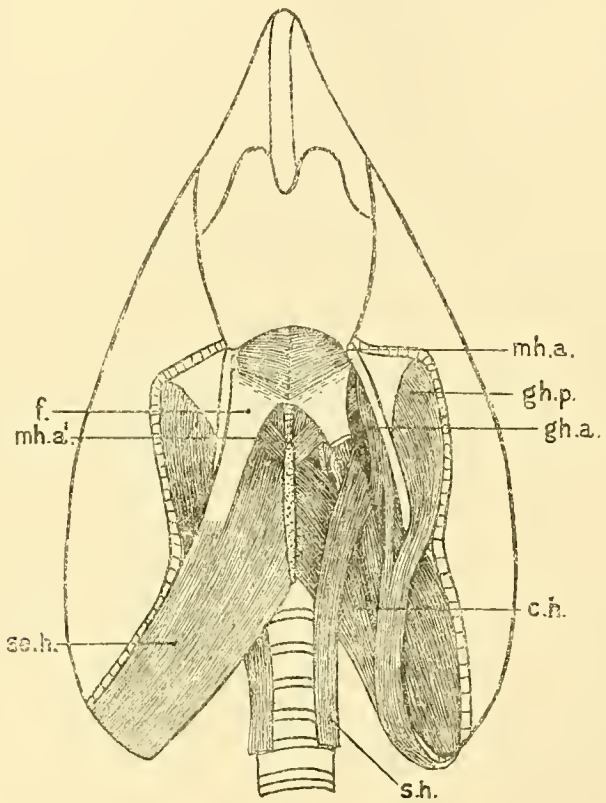
In *Lorius* (text-figs. 12, 14), *Vini*, and *Eos* (Pl. XXVI. fig. 1) the condition foreshadowed in *Pezoporus* has been attained, for the stylohyoideus is absent on both sides. In all three there is a vacancy on the parahyal arch (Pl. XXVII. fig. 21, P.A.) lying between the origin of the thyrohyoideus (*th.h.*) and the insertion of the serpihyoideus (*s.h.*), which corresponds in position with the insertion of the muscle in those Parrots in which it is present; and in *Lorius* there is attached at this part a sheet of connective tissue, ribbon-like in form and of but short extent, which probably represents the last remains of the fascia of the muscle.

In *Nestor* (Pls. XXVII. & XXIX. figs. 22 & 46, *st.h.*) the muscle is very thin and its insertion is unlike that in any other Parrot, and in respect of which it stands alone; it is inserted to the hypocleidium of the completed parahyal arch, immediately anterior to the insertion of the sternohyoideus.

In the majority of Parrots the stylohyoideus is inserted at the apical portion of the parahyal processes; but in *Pyrrhulopsis*, *Loriculus*, *Pezoporus*, *Cyanorhamphus*, and *Tanygnathus* it is inserted behind the apex, so that the free extremities of the parahyal processes extend some little way beyond the anterior margin of the insertion of the muscle. And in *Cyanorhamphus* and *Pyrrhulopsis* the free portions of the processes curve inwards towards the middle line, and in the former Parrot almost meet each other; it strongly suggests a growing forwards of the parahyal processes in order to form the completed parahyal arch of the Loriidæ and *Nestor*.

In *Prioniturus* (text-fig. 16, p. 260) the stylohyoideus (*st.h.*) is tendinous at its insertion, and it is inserted in common with a branch of the sternohyoideus, with which it becomes confluent just before its insertion. In *Stringops* (Pl. XXVII. fig. 18) the stylohyoideus divides into two some distance before reaching its insertion; the posterior branch is inserted at the usual position on the parahyal process, while the anterior one passes towards the middle line and becomes confluent with the internal twig (*th.g.*[1]) of the thyroglossus.

Text-figure 14.



Lorius flavo-palliatus.—Ventral view. On the left the serpihyoideus has been removed, to show the ceratohyoideus (*c.h.*) and sternohyoideus (*s.h.*) and the course of the geniohyoideus (*gh.a.* and *gh.p.*). Other letters as before. (Twice nat. size.)

In *Prioniturus*, *Chrysotis*, *Bolborhynchus*, and *Calopsittacus* the uro-hypobranchial tendon arises directly from the sheath investing the urohyal, as the nodule (N.) that articulates with the ventral surface of that in other Parrots is absent.

A general review of the facts concerning this muscle (posterior mylohyoideus) indicates that its two constituent portions have arisen from a common muscle, since in some Parrots the stylo- and serpihyoideus are confluent along the greater portion of their course, and a gradual separation of the two can be traced. The stylohyoideus

appears to be undergoing retrogression, for in many Parrots its origin is represented by fascia alone, while in others its insertion is reduced to a functionless filament; in *Pezoporus* the muscle of one side of the tongue has disappeared and that of the other is going; and in yet a few others there is a general thinning of the muscle. In *Lorius*, *Eos*, and *Vini* (the only three members of the Loriidæ obtainable) the muscle has completely disappeared, the position of its insertion being indicated in one of them by connective tissue (vestigial fascia) and in the others by a space upon the parahyal process.

In all Parrots, except the Loriidæ, the outer portion of the serpihyoideus is inserted to the uro-hypobranchial tendon, and does not extend beyond it, while in the Loriidæ it is prolonged forwards to an independent insertion at the postero-outer angle of the basihyal. Thus the Loriidæ are characterized by this extended insertion and by the absence of the stylohyoideus muscle.

Nestor occupies a position of isolation with respect to its hypocleidal insertion of the stylohyoideus.

There are indications, in the projection forwards of the parahyal processes beyond the insertion of the stylohyoideus, in certain Parrots of an approach to the Loriidean condition of a completed parahyal arch.

There are all stages in the division of the serpihyoideus into two parts, from an incipient thinning, localized anteriorly and barely perceptible, to a well-defined plane of division passing the whole length of the muscle. In all Parrots but one, the two portions of the muscle persist; but in *Nestor* it is probable that the outer one has disappeared. In certain Parrots the inner portion exhibits a remarkable contraction of its substance at its origin, which in some is not tendinous, but in others markedly so; *Eos* represents the highest specialization in this direction.

Thus the muscle appears to be specializing in two directions: in one, by the complete retrogression of the stylohyoideus, by the division of the serpihyoideus and by the shifting forwards of part of its origin to the basihyal; and in the other direction additionally by the contraction of, and the subsequent formation of, a tendon at the origin of the inner portion.

As far as the characters of the tongue are concerned, we may say that within the Loriidæ—the most specialized family of Parrots—two lines of evolution seem to be mapping themselves: the one exemplified by *Lorius* and *Vini*, and characterized by an uncontracted origin of the serpihyoideus and by the tendon of the ceratoglossus inferior posticus not being fan-shaped at its origin from the muscle; and the other by *Eos*, characterized by the contracted origin of the inner portion of the serpihyoideus and the fan-shaped ceratoglossal tendon. Conditions foreshadowing both these characters of *Eos* are met with in certain of the less specialized Parrots.

Sternohyoideus.

This muscle arises from the anterior end of the ventral border of the sternal carina, and passing forwards along the ventro-lateral aspect of the trachea, on either side, it passes between the ceratohyoideus and posterior mylohyoideus, whence it reaches the dorsal surface of the hyoid and its insertion into the posterior portion of the outer margin of the parahyal processes. In some instances the insertion extends backwards along the body of the basihyal and may even reach to some distance along the hypobranchial. In but very few Parrots (*Eos*, *Ptistes*, *Psittacus*, *Pezoporus*, *Stringops*, and *Aprosmictus* only) is it a continuous muscle from its origin to its insertion; in the majority, the middle portion of that part which extends along the neck is either exceedingly attenuated—represented by a few scattered fibres on the skin—or is quite retrogressed; even in *Eos* and *Aprosmictus* the greater portion of it is attached to the skin of the neck. In a few its origin has retrogressed, and in others distinct evidences of retrogression may be seen at one part or another of its course.

In *Coracopsis*, *Microglossus*, *Cacatua roseicapilla*, *C. sulphurea*, *C. alba*, *C. triton*, and *Eclectus* (text-fig. 7, p. 231) the insertion of the muscle is upon the parahyal process with an extension backwards to the inner surface of the hypobranchial. The muscle divides just before reaching its insertion, the anterior branch becoming inserted to the dorso-lateral surface of the parahyal process and the posterior to the inner surface of the hypobranchial. In *Cacatua triton* the extension is along a little more than the anterior third of the hypobranchial, and is greater than in any other Parrot; in *C. roseicapilla* and *C. alba* the two branches are connected by an intermediate piece of connective tissue, and the posterior branch (that inserted on the hypobranchial) shows signs of retrogression; in *C. sulphurea* the hypobranchial insertion is only represented by a few muscular fibres, it having undergone a great amount of retrogression. In *Microglossus* the hypobranchial insertion is between the ceratoglossus superior and the hypoglossus obliquus, instead of to the inner side of the former muscle. In *Eclectus* (text-fig. 7, p. 231) the parahyal insertion is very broad and extends along the whole length of the parahyal process, while the hypobranchial portion exhibits signs of retrogression as it turns round the ceratoglossus lateralis. In all other Parrots the hypobranchial insertion has disappeared. In *Pyrrhulopsis* the insertion of the muscle into the parahyal process extends backwards along the dorsal surface of the body of the basihyal to the posterior extremity of that. In all other Parrots, *Lorius* (Pl. XXVII. fig. 21, *s.h.*) and *Eos* excepted, the insertion of the muscle is restricted to the parahyal process, and usually to its posterior half; sometimes it is inserted into the lateral surface, and more rarely into the dorsal surface. In *Chrysotis viridigena*, *Eclectus*, and *Cacatua galerita* the insertion extends up to the anterior extremity of the parahyal process. In *Lorius domicella* (Pl. XXVII. fig. 21) and *L. flavo-palliatus* the muscle is inserted to the posterior two-thirds of the parahyal

arch and the dorsal surface of the body of the basihyal; in *Eos* its insertion is limited to the basihyal, and in *Vini* to the posterior half of the parahyal arch. In *Nestor* it is inserted to the parahyal arch just behind the hypocleidium, and is thus more anterior than in the Lories.

In *Ara macao* (Pl. XXVII. fig. 20, *s.h.*) the muscle just before reaching its insertion divides into a larger and a smaller branch, of which the former becomes inserted into the parahyal process and the latter, in common with the hypoglossus obliquus and thyroglossus, into the posterior extremity of the os entoglossum. In *Calyptorhynchus funereus* the muscle just at its insertion becomes confluent with the thyroglossus. In *Pezoporus* (Pl. XXVI. fig. 8, *s.h.*) the muscle narrows and becomes inserted by a small tendon. In *Prioniturus* (text-fig. 16) the muscle divides into two branches, the anterior of which becomes confluent with the stylohyoideus and is inserted with it in a common and tendinous insertion near the apex of the parahyal process, while the latter becomes inserted by a tendinous insertion to the root of that.

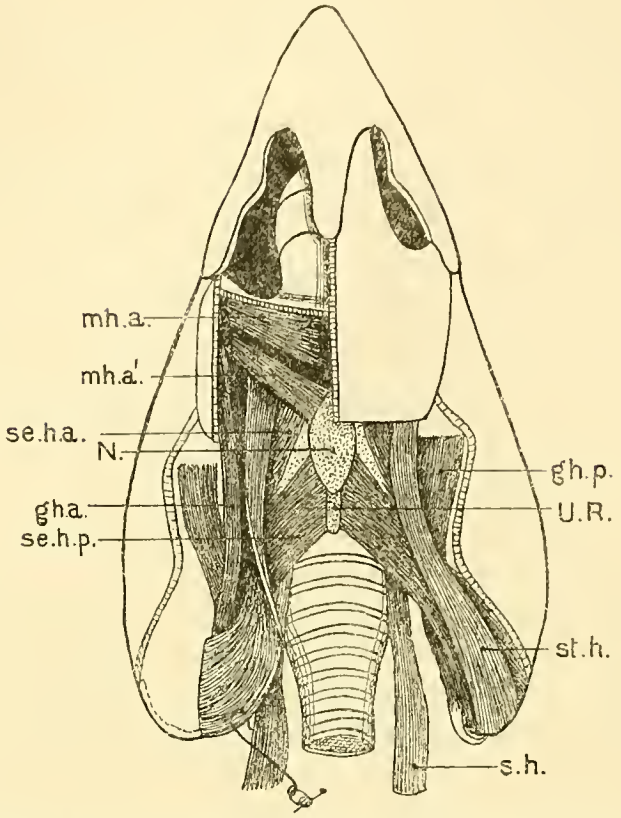
In *Brotogerys* the muscle has retrogressed at the point where it turns round the ceratoglossus lateralis, only the fascia persisting.

In *Ara ararauna* (text-fig. 15), *Platycercus*, *Loriculus*, *Calopsittacus*, and *Cacatua galerita* the origin of the muscle at the carini sterni has undergone complete retrogression, and in the first- and last-named Parrot it is represented by a narrow tract of fat. In *Bolborhynchus*, *Psittacula*, *Nasiterna*, and *Tanygnathus* the origin is represented by a mere trace of muscular tissue; while in *Conurus holochlorus*, *Eclectus*, *Chrysotis æstiva*, *C. viridigena*, *C. ochrocephala*, *Pœocephalus*, and *Conurus jendaya* it is somewhat stouter, but still very narrow. In *Palæornis* and the remaining Parrots it is well defined; and in *Nestor* it is very strongly developed. In *Stringops*, in correlation with the absence of a carini sterni, the muscle arises from the skin of the thorax in this region by three strands which soon unite to form a single trunk.

In *Eos*, *Ptistes*, *Aprosmictus*, *Pezoporus*, *Psittacus*, and *Stringops* the muscle is continuous from its origin to insertion. In *Stringops* it remains free of the skin throughout its course, but in all other Parrots it is attached to that along the greater portion of its course. In the six Parrots just mentioned it widens and thins in its mid-cervical region, except in *Eos*, in which it thickens as well as widens. In *Lorius domicella*, *L. flavo-palliatus*, *Chrysotis ochrocephala*, and *Nestor* it becomes exceedingly attenuated in the mid-cervical region. In all the remaining Parrots the muscle has undergone retrogression in this region, usually disappearing about half an inch to an inch from its origin, and reappearing a little posterior to the hinder edge of the serpihyoideus.

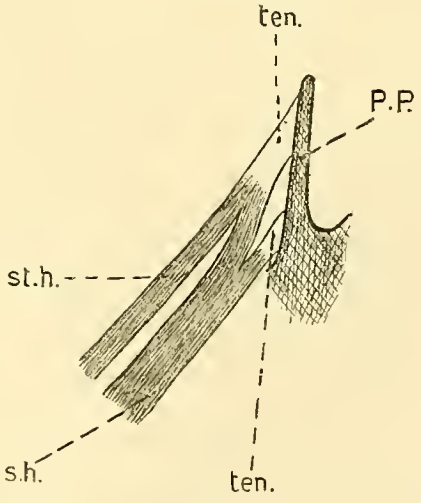
Primitively, the muscle thus appears to have been a continuous one from its origin to insertion, but it has undergone more or less extensive retrogression, principally in the mid-cervical region, but also at its origin and insertion. Its insertion appears to

Text-fig. 15.



Ara ararauna.—Ventral view. On the right, half the lower bill has been removed and the stylohyoideus (*st.h.*) reflected to show the course of the geniohyoideus (*gh.a*). (Nat. size.)

Text-fig. 16.



Prioniturus.—Dorsal view, to show the connection between the sternohyoideus (*s.h.*) and the stylohyoideus (*st.h.*) near their insertions to the parahyal process (P.P.). (Much enlarged.)

have been of a much more extensive nature primitively, but it has retrogressed in the majority of Parrots along its hypobranchial and basihyal portions, leaving only its parahyal process part.

Geniohyoideus.

In Parrots this muscle has reached a stage not known to have been attained in other birds. In *Chauna*, *Rhytidoceros*, *Cygnus*, *Pelecanus*, *Lophophorus*, *Palamedea*, *Corvus*, *Anser*, *Procellaria*, and *Spheniscus* this muscle is known to be single. In *Nectarinia*, *Otis*, *Rhea*, *Struthio*, *Dromæus*, *Rhynchotus*, *Ciconia*, and *Opisthocomus* it is double (8 & 9). In some Parrots the muscle consists of two divisions, but in the majority it is composed of three, which have arisen from the primitive set of two, by the splitting longitudinally of the anterior one of these.

The most posterior division of the muscle arises from either the ventral margin of the rami of the mandible (text-fig. 10, *gh.p*), usually about one-third of the way behind the hinder margin of the lower bill, or from the outer surface of the latter (text-fig. 12, p. 251). The two portions of the anterior division arise from a common origin at the inner surface of the antero-dorsal portion of the lower jaw (text-fig. 11, *gh.a*^{1}., *gh.a*^{2}.), just posterior to and slightly ventrad of the origin of the mylohyoideus anterior; they are usually bound together by connective tissue. The posterior portion is inserted into the dorsal surface of the ceratobranchial (Pl. XXVII. fig. 12, *gh.p*.); the anterior division of the anterior muscle (*gh.a*^{1}.) into the posterior extremity of the hypobranchial, folding round its dorsal and ventral surfaces, and the posterior division (*gh.a*^{2}.) into the ventral surface of the ceratobranchial.

In *Lorius* (text-fig. 12, p. 251, and Pl. XXVII. fig. 21), *Eos*, *Vini*, *Prioniturus*, *Chrysotis æstiva*, *C. ochrocephala*, *Pœocephalus rüppelli*, *Ptistes*, *Ara ararauna* (Pl. XXVIII. fig. 24), *Psittacus*, *Cyanorhamphus*, *Psephotus*, *Nasiterna*, *Eclectus*, *Loriculus*, *Palæornis*, *Caica*, *Platycercus*, and *Tanygnathus* the muscle consists of three divisions, the anterior two of which are usually closely bound together with connective tissue at their common origin. In *Prioniturus*, *Psephotus*, *Eclectus*, and *Tanygnathus* the outer one of the two anterior portions has developed a small tendon at its origin.

In *Stringops* and *Brotogerys* the anterior muscle is divided into two along the greater portion of its length, but at its origin and for some distance behind it is a single muscle. In *Pezoporus*, *Pœocephalus robustus*, *Pionopsittacus*, *Psittacula*, and *Cyanolyseus* the anterior muscle is more or less divided into two in a longitudinal direction.

In *Chrysotis panamensis*, *Cacatua sulphurea*, *C. roseicapilla*, *C. leadbeateri*, *C. galerita*, *Calopsittacus*, *Psittinus*, *Ara macao*, *Conurus jendaya*, *Bolborhynchus*, and *Calyptorhynchus* the muscle is primitive and consists of only two divisions, a single anterior

and a posterior one. In *Conurus jendaya* and *Cacatua galerita* the anterior portion is very indistinctly divided into two.

In *Lorius domicella* (text-fig. 12), *Vini*, *Prioniturus*, *Chrysotis*, *Ptistes*, *Nasiterna*, *Bolborhynchus*, *Loriculus*, *Pyrrhura*, *Brotogerys* (text-fig. 13), *Palæornis*, *Platycercus*, and *Tanygnathus* the posterior division of the muscle arises from the ventral margin of the rami of the mandible. In *Lorius flavo-palliatus* (text-fig. 14), *Conurus jendaya* (text-fig. 10), *Eos*, *Stringops*, *Pezoporus*, *Pæocephalus*, *Ara*, *Psittacus* (Pl. XXVI. fig. 3), *Psittacula*, *Eclectus*, *Cyanolyseus*, *Coracopsis*, and *Cacatua* it arises from the outer surface of the rami.

In *Nestor notabilis* the muscle consists of two divisions only, but they become confluent at their insertion (Pl. XXIX. fig. 46), and form a tubular investment round the extremity of the hypobranchial and the whole length of the ceratobranchial.

The Genioglossus Muscle.

This is a paired muscle arising from the inner surface of the posterior end of the lower bill, immediately on either side of the middle line. Each half passes upwards and forwards, and becomes inserted (Pl. XXIX. fig. 50, *gg.*) into a thin ridge which marks the dorsal limit of the posterior lateral process of the entoglossum (*cf.* P. Z. S. 1895, p. 166). It has fundamentally the same arrangement in all Parrots, except *Nestor*, in which the two portions of the muscle pass dorsally to the entoglossum and become confluent with each other in the middle line, so that there is no insertion to the entoglossum; the muscle merely forms a loop round it.

The Ceratohyoideus Muscle.

This muscle exhibits but little variation. Its origin in some instances (Pl. XXVIII. fig. 28) is entirely from the sheath investing the urohyal; in others it is partly from that and partly from the posterior border of the uro-hypobranchial tendon; and in a few (Pl. XXVIII. fig. 24) it is partly from the nodule (N.) on the ventral surface of the urohyal and partly from the uro-hypobranchial tendon (*u.ten.*). Its insertion in all cases is into the inner surface of the hypobranchial, ventrad of the origin of the ceratoglossus inferior posticus, sometimes towards its anterior and at others towards its posterior end.

In *Microglossus*, *Tanygnathus*, *Pyrrhulopsis*, *Platycercus*, *Pæocephalus rüppelli*, *Cacatua*, *Nestor*, *Psittacus*, *Psephotus*, *Conurus holochlorus*, *Coracopsis*, and *Brotogerys* (Pl. XXVIII. fig. 33, *ch.*) it arises entirely from the urohyal sheath. In *Calyptorhynchus*, *Palæornis*, *Loriculus*, *Eclectus*, *Bolborhynchus*, *Psittacula*, *Nasiterna*, *Cyanorhamphus*, *Pyrrhura*, *Pionopsittacus*, *Ptistes*, *Psittinus*, *Conurus jendaya*, *C. cactorum*, *Pezoporus*, *Cyanolyseus*, *Stringops*, *Calopsittacus*, and *Prioniturus* it arises partly from the urohyal

sheath and partly from the uro-hypobranchial tendon; in *Cyanorhamphus* and *Stringops* it arises mainly from the uro-hypobranchial tendon, and in *Calyptorhynchus* chiefly from the urohyal sheath. In *Chrysotis* (Pl. XXVIII. fig. 28), *Caica*, and *Deroptyus* it arises in main part from the anterior two-thirds of the urohyal, and to a small extent from the posterior border of the basihyal. In *Ara*, *Pœocephalus robustus*, *Lorius* (Pl. XXIX. fig. 37, *ch.*), *Eos* (Pl. XXIX. fig. 39), and *Vini* it arises in part from the nodule on the ventral surface of the urohyal, and in part from the uro-hypobranchial tendon.

In *Pezoporus* and *Pyrrhulopsis* there is developed along the inner side at the anterior end of the muscle a small tendinous tract, which extends about half its length.

In *Eclectus*, *Ara*, *Cacatua triton*, and *C. alba* the muscle is inserted along the anterior half of the hypobranchial. In *Microglossus*, *Prioniturus*, *Cacatua galerita*, *C. leadbeateri*, and *C. roseicapilla* it is inserted into the anterior two-thirds; and in *Pyrrhulopsis*, *Nestor*, and *Calyptorhynchus* into the posterior two-thirds. In *Lorius* (Pl. XXIX. fig. 37), *Eos*, *Vini*, *Brotogerys* (Pl. XXVIII. fig. 33), *Loriculus*, *Conurus holochlorus*, *Nasiterna*, *Psittacus*, *Ptistes*, *Psittinus*, *Pœocephalus*, *Pezoporus*, *Stringops*, *Calopsittacus*, *Deroptyus*, and *Chrysotis* it is inserted along nearly the whole length of the bone.

The Mesoglossus Muscle.

This muscle has not been previously described. It is triangular in form, with its apex directed backwards, and connected with the superior ceratoglossals in a manner already described (*ante*, p. 227). It lies in the dorsal concavity of the entoglossum (Pl. XXVI. fig. 11, *mg.*, and Pl. XXIX. fig. 50, *mg.*), and is attached on the one hand to the superior ceratoglossals, and on the other to the hypoglossus rectus and the membrane of the extremity of the tongue. In comparatively very few Parrots it is wholly muscular in nature; in the greater number it is composed of muscle-fibres and a dense connective tissue, in varying proportions, inextricably mixed together; in yet a large number still it is wholly composed of connective tissue of a very dense and resistant nature; and in one or two it is represented by a connective-tissue membrane only. The muscle, or that which represents it, is invested by a thick fascia.

In *Nestor* (Pl. XXVII. fig. 22, mg^1.) and *Calyptorhynchus* the muscle is not represented, except by a thick membranous sheet of white fibrous tissue. In *Platycercus*, *Cacatua* (Pl. XXVII. fig. 13, mg^1.), *Conuras*, *Calopsittacus*, *Psittinus*, *Stringops* (Pl. XXVII. fig. 18), *Pyrrhura* (Pl. XXVII. fig. 19), *Psittacula*, *Bolborhynchus*, *Cyanolyseus*, and *Brotogerys* it is represented by a mass of dense, white, fibrous tissue, invested in a tough sheath; in the tissue of *Cacatua triton* branched pigment-cells are present. In *Microglossus*, *Pyrrhulopsis*, *Eclectus* (text-fig. 7, p. 231), *Palæornis*, and *Tanygnathus* muscles-fibres have appeared in the mass of fibrous tissue; in *Chrysotis* (Pl. XXVII.

fig. 14, *mg.*), *Pezoporus* (Pl. XXVI. fig. 8, *mg.*), *Nasiterna*, *Deroptyus*, and *Loriculus* the muscle-fibres are slightly more abundant, and about equal in quantity to the fibrous tissue ; and in *Prioniturus*, *Pœocephalus* (Pl. XXVI. fig. 10), *Pionopsittacus*, and *Caica* the muscle-fibres predominate. In *Microglossus* I found in the substance of the muscle some oval sacs containing an axillary strand and some very small cells with processes; they are probably sensory in nature and deserve investigation by modern methods. In *Ptistes*, *Ara* (Pl. XXVII. fig. 20), *Psittacus*, *Coracopsis*, *Cyanorhamphus*, and *Psephotus* the muscular element constitutes nearly the whole of the muscle, though the amount of connective tissue present is greater than one would expect to find usually. In *Lorius* (Pl. XXVII. fig. 21), *Eos*, and *Vini* the muscle is well developed and of a normal nature.

THE CLASSIFICATION OF PARROTS ACCORDING TO THEIR LINGUAL MYOLOGY AND OSTEOLOGY.

LORIIDÆ.

(A.) Parahyal arch complete. Stylohyoideus absent. Outer portion of serpihyoideus inserted to basihyal. Ceratoglossus inferior posticus extends back to posterior end of hypobranchial. A ceratoglossus inferior anticus accessorius absent.

Eosinæ.

(1) The tendon of the ceratoglossus inferior spreads out in a fan-shaped manner over the posterior portion of the muscle. Inner division of serpihyoideus contracted at origin.

Eos.

Lorinæ.

(2) The tendon of inferior ceratoglossus is merely continued back on to the ceratoglossus inferior posticus, without widening. Serpihyoideus is not contracted at origin.

Lorius.

Vini.

NESTORIDÆ.

(B.) Parahyal arch complete. Stylohyoideus narrow, inserted to hypocleidium of parahyal arch, and not confluent with serpihyoideus at any part of its course. Outer (anterior) portion of serpihyoideus not represented. Ceratoglossus inferior posticus does not extend back to posterior end of hypobranchial. The posterior division of anterior mylohyoideus absent.

Nestor.

(C.) Parahyal arch incomplete. Stylohyoideus usually well developed, and inserted to or near apical portion of parahyal process. Outer portion of serpihyoideus inserted to head of hypobranchial. The ceratoglossus

[To face p. 264.

THE CLASSIFICATION OF PARROTS ACCORDING TO THEIR LINGUAL MYOLOGY AND OSTEOLOGY.

LORIIDÆ

(A.) Parahyal arch complete. Stylohyoideus absent. Outer portion of serpihyoideus inserted to basihyal. Ceratoglossus inferior posticus extends back to posterior end of hypobranchial. A ceratoglossus inferior anticus accessorius absent.

Eosinæ

(1) The tendon of the ceratoglossus inferior spreads out in a fan-shaped manner over the posterior portion of the muscle. Inner division of serpihyoideus contracted at origin.

Eos.

Lorinæ

(2) The tendon of inferior ceratoglossus is merely continued back on to the ceratoglossus inferior posticus, without widening. Serpihyoideus is not contracted at origin.

Lorius.

Vini.

NESTORIDÆ

(B.) Parahyal arch complete. Stylohyoideus narrow, inserted to hypoclidium of parahyal arch, and not confluent with serpihyoideus at any part of its course. Outer (anterior) portion of serpihyoideus not represented. Ceratoglossus inferior posticus does not extend back to posterior end of hypobranchial. The posterior division of anterior mylohyoideus absent.

Nestor.

PSITTACIDÆ

(C.) Parahyal arch incomplete. Stylohyoideus usually well developed, and inserted to or near apical portion of parahyal process. Outer portion of serpihyoideus inserted to head of hypobranchial. The ceratoglossus inferior posticus may or may not extend back to the posterior end of the hypobranchial, and exceptionally may be absent. A ceratoglossus inferior anticus accessorius, with but one exception, present.

Group I.

1. The ventral fascia of the ceratoglossus inferior anticus is not tendinous: the ceratoglossus inferior posticus extends back to the posterior end of the hypobranchial = $\frac{3}{3}$.

Psittacellinæ

(*a*) The thyroglossus arises from the parahyal process.

(*α*) The inner portion of the ceratoglossus inferior anticus has reached stage III of retrogression.

Psittacula.

Cyanorhamphus.

Nymphicus.

(*b*) The inner portion of the ceratoglossus inferior anticus has reached stage II of retrogression.

Pyrrhulopsis.

Caica.

Pyrrhurinæ

(*β*) The thyroglossus arises from the entoglossum.

(*a*) The inner portion of the ceratoglossus inferior anticus has reached stage III of retrogression.

Loriculus.

Pyrrhura.

(*b*) The inner portion of the ceratoglossus inferior anticus has reached stage II of retrogression.

Group II.

II. The ventral fascia of the ceratoglossus inferior anticus is tendinous.

(1) The tendon of the ceratoglossus inferior is well developed, and the ceratoglossus inferior posticus extends back to the posterior end of the hypobranchial = $\frac{3}{3}$.

Polytelinæ

(*a*) The thyroglossus arises from the parahyal process.

Pezoporus.

Platycercus.

Bolborhynchus.

Prioniturus.

Tanygnathinæ

(*β*) The thyroglossus arises from the entoglossum.

Pœocephalus.

Tanygnathus.

Psistes.

Psittinus.

(2) The tendon of the ceratoglossus inferior is not well developed.

Conurinæ

(*a*) The ceratoglossus inferior posticus extends back to the posterior end of the hypobranchial = $\frac{3}{3}$.

Pœcilotus.

Conurus.

Palæornis.

Brotogerys?

Psittacinæ

(*β*) The ceratoglossus inferior posticus extends back along the anterior two-thirds only of the hypobranchial = $\frac{2}{3}$.

Deroptyus.

Psittacus.

Eclectinæ

(*γ*) The ceratoglossus inferior posticus extends back along the anterior half only of the hypobranchial = $\frac{1}{2}$.

Eclectus.

Coracopsis.

(3) The tendon of the ceratoglossus inferior posticus is not developed, and a thickened tract in the tendinous fascia foreshadowing its formation may or may not be present.

Chrysotinæ

(*a*) The thyrohyoideus accessorius is absent.

Cyanolyseus.

Chrysotis.

Ara.

Cacatuinæ

(*β*) The thyrohyoideus accessorius is present.

Cacatua.

Stringops.

Microglossus.

Calopsittacus.

Nasiterna.

Calyptorhynchus.

TABULATION OF THE CHARACTERS OF THE MORE IMPORTANT MUSCLES, AND THE ARRANGEMENT OF THE GENERA DESCRIBED, INTO STAGES ACCORDING TO THE DEGREE OF DEVELOPMENT OF THE TENDON OF THE CERATOGLOSSUS INFERIOR.

PA = Parahyal arch.
PP′ = Parahyal process origin (primitive condition).
PP = Parahyal process origin (secondary condition).
OE = Entoglossum.
HB = Hypobranchial.
OL = The thyroglossus has lost its origin and lies free in the entoglossal concavity or is attached to the membrane of the tongue.
OL & PP′ = The thyroglossus has split and its origin is partly from parahyal process (primitive condition) and partly it is as in OL.
— = Absent.
P = Present.
D = Divided.
U = Single or undivided.
F.S. = Fairly strongly developed.
T.F. = Tendinous fascia.
W.T.F. = Weak tendinous fascia.
T.T. = Tendinous tract.
S. = Strongly developed.
V.S. = Very strongly developed.
B. = Broad.
Absent = Tendon or tendinous fascia absent.
CG.I.A^1. = Inner portion of ceratoglossus inferior anticus.
CG.L. = Ceratoglossus lateralis.
TH.H.A. = Thyrohyoideus accessorius.
HG.O. = Hypoglossus obliquus.
TH.G. = Thyroglossus.
$\frac{3}{3}$ = Extension along the whole length of the hypobranchial.
$\frac{2}{3}$ = }
$\frac{1}{3}$ = } Extension along that fraction of the length of the hypobranchial (anterior end implied).
$\frac{1}{2}$ = }
$\frac{1}{4}$ = }
$\frac{2^N}{3}$ = A little less than $\frac{2}{3}$, but more than $\frac{1}{2}$.
$\frac{2'}{3}$ = A little more than $\frac{2}{3}$.
O = The inner portion of the ceratoglossus inferior anticus is most fully developed, and reaches not only to the middle line of the basihyal but extends back along the urohyal. (Retrogression has not commenced.)
I = As in O, but does not extend back along the urohyal.
II = That stage of retrogression when the muscle no longer reaches the middle line and does not extend inwards more than about midway between I and III, *i. e.* midway between the tendon of the ceratoglossus inferior and the middle line.
III = The inner portion has undergone complete retrogression, so that the ceratoglossus inferior anticus does not extend to the inner side of its tendon (cg.i.a^1. has wholly disappeared).
0 = Absence of ceratoglossus inferior posticus and implies a "unipars" type of muscle.

	The Evolution of the Tendon of the Ceratoglossus inferior.	The extension of the Ceratoglossus inferior posticus along the Hypobranchial.	The amount of Retrogression of CG.I.A[1].
	Stage 9.		
Eos riciniata	As in the stage next below, but the tendon spreads out in a fan-like form over the surface of the ceratoglossus inferior posticus.	$\frac{3}{3}$	III
	Stage 8.		
Vini australis	As in the stage next below, but the tendons are more strongly developed and extend more posteriorly.	$\frac{3}{3}$	III
Lorius flavo-palliatus		$\frac{3}{3}$	II
„ *domicella*		$\frac{3}{3}$	III
	Stage 7.		
Caica	The ventral fascia of the ceratoglossus inferior anticus is no longer tendinous, so that the tendons of this muscle and of the lateral ceratoglossal are separated, except at their common origin.	$\frac{3}{3}$	II
Psittacula		$\frac{3}{3}$	between II & III
Cyanorhamphus		$\frac{3}{3}$	III
Nymphicus		$\frac{3}{3}$	III
Pyrrhulopsis splendens		$\frac{3}{3}$	between I & II
„ *personata*		$\frac{3}{3}$	II
Loriculus		$\frac{3}{3}$	between II & III
Pyrrhura		$\frac{3}{3}$	III
	Stage 6.		
Pezoporus	The ventral fascia of the ceratoglossus inferior anticus is still tendinous, but the tendon is more strongly developed than in the stage next below.	$\frac{3}{3}$	III
Platycercus		$\frac{3}{3}$	III
Bolborhynchus		$\frac{3}{3}$	between II & III
Prioniturus		$\frac{3}{3}$	II
Tanygnathus		$\frac{3}{3}$	II
Pionopsittacus		$\frac{3}{3}$	I
Psittinus		$\frac{3}{3}$ nearly	II
Pœocephalus robustus		$\frac{3}{3}$	II
„ *rüppelli*		$\frac{3}{3}$	III
Ptistes		$\frac{1}{2}$ & $\frac{3}{3}$	II
Nestor notabilis		$\frac{3}{3}$	I
	Stage 5.		
Psephotus	To a slight extent the thickened tract in the ventral fascia of the stage next below has separated from it and is partially a distinct tendon. The	$\frac{3}{3}$	III
Deroptyus		$\frac{2}{3}$?	II
Conurus holochlorus		$\frac{3}{3}^{N}$	II
„ *jendaya*		$\frac{3}{3}^{N}$	III

Extension of CG.L. along HB.	Extension of HG.O. along HB.	The HG.O. Divided or Undivided.	Degree of Development of Tendon of HG.O.	Presence or Absence of TH.H.A.	Origin of TH.G.
$\frac{3}{3}^{N}$	$\frac{3}{3}^{N}$	D	V.S.	—	PA
$\frac{3}{3}^{N}$	$\frac{3}{3}^{N}$	D	S.	—	PA
$\frac{3}{3}^{N}$	$\frac{3}{4}$	D	S.	—	PA
$\frac{3}{3}^{N}$	$\frac{2}{3}$	D	S.	—	PA
$\frac{3}{3}$	$\frac{3}{3}^{N}$	D	S.	—	PP
$\frac{1}{2}'$	$\frac{3}{3}^{N}$	D	S.	—	PP
$\frac{3}{3}^{N}$	$\frac{3}{3}^{N}$	U	V.S.	—	PP
$\frac{2}{3}$	$\frac{2}{3}$	D	S.	—	PP
$\frac{2}{3}$	$\frac{1}{2}$	D	S.	—	PP
$\frac{2}{3}$	$\frac{1}{2}$	D	S.	—	PP
$\frac{2}{3}$	$\frac{2}{3}$	D?	F.S.	—	OE
$\frac{3}{3}^{N}$	$\frac{2}{3}$	U	F.S.	—	OE
$\frac{3}{3}^{N}$	$\frac{3}{3}$	D	S. & B.	—	PP
$\frac{3}{3}^{N}$	$\frac{2}{3}'$	D	F.S.	—	PP
$\frac{3}{3}^{N}$	$\frac{3}{3}^{N}$	U	S.	—	PP
$\frac{3}{3}^{N}$	$\frac{3}{3}^{N}$	D (incipient)	S. & B.	—	PP
$\frac{2}{3}'$	$\frac{1}{2}$	D	W.	—	OE
$\frac{2}{3}$ & $\frac{3}{3}$ (between)	$\frac{3}{3}$	D	S. & B.	—	OE
$\frac{2}{3}$ & $\frac{3}{3}$ (between)	$\frac{2}{3}^{N}$	D	S.	—	OE
$\frac{1}{2}$	$\frac{1}{3}$	D	T.F.) at insertion	P	OE & PP
$\frac{2}{3}$*	$\frac{1}{3}$	D	T.F.) only.	—	OE & PP
$\frac{3}{3}^{N}$	$\frac{3}{3}^{N}$	D	F.S.	—	OE
$\frac{1}{2}$	$\frac{1}{2}$	U	S.	P	OL
$\frac{1}{2}$	$\frac{2}{3}$	U	W.	—	PP
$\frac{1}{2}$	$\frac{2}{3}^{N}$	U	Absent.	—	OE & PP
$\frac{3}{3}^{N}$	$\frac{1}{3}$	D	F.T.S. & B.	—	OE & PP
$\frac{3}{3}^{N}$	$\frac{2}{3}^{N}$	D	W.T.F.	—	OE

TABLE

	The Evolution of the Tendon of the Ceratoglossus inferior.	The extension of the Ceratoglossus inferior posticus along the Hypobranchial.	The amount of Retrogression of CG.I.A[1].
	Stage 5 (*continued*).		
Conurus cactorum	thickened tract is slightly more pronounced.	$\frac{3}{3}^{N}$	I
Palæornis torquata		$\frac{3}{3}$	between II & III
Brotogerys (right hand)		$\frac{3}{3}^{N}$	II
Psittacus		$\frac{2}{3}$	II
Eclectus		$\frac{1}{2}$	II
Coracopsis		$\frac{1}{2}$	I
	Stage 4.		
Chrysotis viridigena	The ceratoglossus inferior posticus	$\frac{2}{3}$	between I & II
„ *æstiva*	is inserted to a slightly thickened,	$\frac{2}{3}$	II
„ *panamensis*	elongated tract in the ventral ten-	$\frac{1}{2}$	I
„ *ochrocephala*	dinous fascia of the ceratoglossus	$\frac{2}{3}$	II
Cyanolyseus patagonicus	inferior anticus. This tract fore-	$\frac{1}{3}$	I
Ara macao	shadows the formation of the distinct	$\frac{1}{3}$	I
Microglossus	tendon of higher stages.	$\frac{1}{3}$	I
Cacatua triton		$\frac{1}{3}$	0
	Stage 3.		
Stringops	The ceratoglossus inferior posticus	$\frac{1}{3}$	0
Nasiterna pusio	has separated from the parent muscle	$\frac{1}{3}$	I
Calopsittacus	(*cg.i.a*), but is still connected with	$\frac{2}{3}$	I
Cacatua leadbeateri	the tendinous fascia of that.	$\frac{2}{3}$	0
„ *sulphurea*		$\frac{1}{3}$	0
	Stage 2.		
Cacatua galerita	The ceratoglossus inferior anticus has grown back upon the hypobranchial, and forms a very rudimentary ceratoglossus inferior posticus. Otherwise as in Stage 1.	$\frac{1}{4}$	0
	Stage 1.		
Ara ararauna	The muscle is composed of the	0	I
Cacatua roseicapilla	ceratoglossus inferior anticus only;	0	0
„ *alba*	the inner part is strongly developed,	0	0
Calyptorhynchus funereus	and the ventral fascia is tendinous.	0	0
„ *banksii*		0	0

(continued).

Extension of CG.L. along HB.	Extension of HG.O. along HB.	The HG.O. Divided or Undivided.	Degree of Development of Tendon of HG.O.	Presence or Absence of TH.H.A.	Origin of TH.G.
$\frac{2}{3}^{N}$	$\frac{1}{2}$	U	Absent.	—	OE
$\frac{2}{3}$	$\frac{2}{3}$	D	W.	—	OE
$\frac{2}{3}'$	To head of HB.	U	Absent.	—	OE
$\frac{1}{2}$	,, ,,	D	,,	—	OL & PP′
$\frac{2}{3}^{N}$	$\frac{1}{3}$	U	W.	P	OL
$\frac{2}{3}$	$\frac{1}{3}$	U	W.T.T.	—	PP′
$\frac{2}{3}$	$\frac{1}{2}^{N}$	D	T.F. at origin.	—	Intermediate between OE & OL
$\frac{2}{3}$	$\frac{1}{2}$	D	,, ,,	—	OL
$2'$	$\frac{1}{3}$	D	S. & B.T.T.	—	OL
3^{N}	$\frac{1}{2}^{N}$	D	W.T.T.	—	OL
$\frac{1}{2}$	$\frac{1}{2}$	D	W.T.F.	—	OE
$\frac{1}{2}$	Head of HB.	U	F.T.	—	OE
$\frac{1}{2}^{N}$	,, ,,	D	Absent.	P	OL
$\frac{1}{2}^{N}$	,, ,,	D	,,	P	OL & PP′
$\frac{1}{2}$	To head of HB.	U	F.T.	P	OL & PP′
$\frac{1}{2}$	$\frac{1}{3}^{N}$	D	....	P	OL & PP′
$\frac{2}{3}$	Head of HB.	U	F.T.	P	OL
$\frac{1}{3}$	$\frac{1}{3}^{N}$	U	Absent.	P	OL
$\frac{1}{2}$	$\frac{1}{3}$	U	,,	P	OL
$\frac{1}{2}$	$\frac{1}{3}$	U	Absent.	P	OL
$\frac{1}{2}$	$\frac{1}{2}^{N}$	U	F.T.	—	OE
$\frac{1}{2}$	$\frac{1}{3}$	U	Absent.	P	OL
$\frac{1}{3}$	Head of HB.	U	,,	P	OL & PP′
$\frac{1}{3}$	,, ,,	U	,,	P	OL & PP′
$\frac{1}{2}$	,, ,,	D	,,	P?	OL & PP′?

Leading References alluded to in the Text.

(1) C. Giebel.—Die Zunge der Vögel und ihr Gerüst mitgetheilt. Zeit. für Naturwiss. vol. xi. 1858, p. 19.

(2) Chr. Nitzsch.—Zur Anatomie der Papageien, nach Chr. Nitzsch's Untersuchungen mitgetheilt vom C. Giebel. Zeit. für Naturwiss. vol. xix. 1862, p. 133.

(3) R. W. Shufeldt.—Osteology of *Conurus carolinensis*. Journ. Anat. & Phys. vol. xx. 1886, p. 407.

(4) H. Gadow.—Bronn's Klass. und Ordnung. d. Thier-Reichs. "Vögel," 1891, i. Anat. Theil.

(4′) H. Gadow.—Bronn's Klass. und Ordnung. d. Thier-Reichs. "Vögel," 1893, ii. System. Theil.

(5) Beddard and Parsons.—On certain Points in the Anatomy of Parrots bearing on their Classification. P. Z. S. 1893.

(6) St. George Mivart.—On the Hyoid Bone of certain Parrots. P. Z. S. 1895.

(7) St. George Mivart.—On the Hyoid Bone of *Nestor* and *Lathamus*. P. Z. S. 1896.

(8) P. Chalmers Mitchell.—A Contribution to the Anatomy of the Hoatzin. P. Z. S. 1896.

(9) R. W. Shufeldt.—The Myology of the Raven. London and New York, 1890.

(10) Beddard and Chalmers Mitchell.—On the Anatomy of *Palamedea cornuta*. P. Z. S. 1894, p. 536.

(11) T. Salvadori.—Catalogue of Parrots in the Collection of the British Museum (Cat. Birds, vol. xx.). 1891.

(12) F. E. Beddard.—The Structure and Classification of Birds. London, New York, and Bombay, 1898.

INDEX TO LETTERING ON PLATES.

ce. = point of origin of cg.i^1. from cg.i.a.
cg.i^1. = ceratoglossus inferior anticus accessorius.
cg.i^2. = „ „ „ „ secundus.
cg.i^3. = part of cg.i.p. becoming or that has become separated from the parent muscle.
cg.i.a. = ceratoglossus inferior anticus.
cg.i.a^1. = inner portion of cg.i.a.
cg.i.a^2. = the part of cg.i.a. that arises from the urohyal.
cg.i.p. = ceratoglossus inferior posticus.
cg.i.p^1. = the posterior extension of cg.i.a. that forms the rudiment of cg.i.p.
cg.l. = ceratoglossus lateralis.
cg.s. = „ superior.
cg.ss. = „ sub-superior.
cg.s.a. = „ superior accessorius.
ch. = ceratohyoideus.
c.t. = connective tissue.
f. = persistent fascia of the retrogressed portion of the anterior division of the anterior mylohyoideus.
f.p. = persistent fascia of the retrogressed portion of the posterior division of the anterior mylohyoideus.
gg. = insertion of genioglossus.
gh.a. = anterior geniohyoideus.
gh.a^1. & gh.a^2. = anterior and posterior divisions of gh.a.
gh.p. = posterior geniohyoideus.
hg.o. = hypoglossus obliquus.
hg.r. = „ rectus.
ins. = insertion of outer extremity of anterior division of serpihyoideus.
m. = membrane of tongue.
mh.a. & mh.a^1. = anterior and posterior divisions respectively of anterior mylohyoideus.
mg. & mg^1. = mesoglossus or tissue occupying place of mesoglossus respectively.
se.h. = serpihyoideus.
se.h.a. = anterior division of serpihyoideus.
se.h.p. = posterior „ „
se.h., st.h. = common origin of serpihyoideus and stylohyoideus.
s.h. = sternohyoideus.
st.h. = stylohyoideus.
ten. = tendon joining the mesoglossus and superior ceratoglossus.
tg. = tongue.
th.h. = thyrohyoideus.
th.h.a. = „ accessorius.
th.h.a.t. = „ „ transversalis.
th.g. = thyroglossus.
th.g^1. = that part of thyroglossus which has withdrawn from its origin at the parahyal process.
u.ten. = uro-hypobranchial tendon.
α = ceratoglossus inferior posticus ventralis.
β = „ „ „ dorsalis.
γ = „ „ „ medius.
AD^1. = anterior end of antero-posterior ridge of basihyal.
A.L.P. = anterior lateral process of entoglossum.
BH. = basihyal.
CB. = ceratobranchial.
EN. = entoglossum.
HB. = hypobranchial.
P.A. = parahyal arch.
P.P. = „ process.
N. = nodule (sometimes bony, but usually cartilaginous) articulating with the ventral surface of urohyal at its root.
UR. = urohyal.
T. = trachea.

PLATE XXVI.

PLATE XXVI.

Fig. 1. *Eos riciniata.* Ventral view, after removal of the skin. On the left the inner portion of serpihyoideus has been removed and the muscles slightly separated to show their relations in the otherwise undisturbed condition. (Magnified $1\frac{1}{2}$.)

Fig. 2. *Stringops habroptilus.* Ventral view, after removal of the skin. (Reduced $\frac{1}{3}$.)

Fig. 3. *Psittacus crithacus.* Ventral view. On the left, one-half of the lower bill has been removed, as well as the persistent fascia (*f.*), which is a backward prolongation of the anterior portion of the anterior mylohyoideus. (Reduced $\frac{1}{4}$.)

Fig. 4. *Cacatua galerita.* Ventral view. The fascia (*f.*) of the left side has been removed to show the similar but very unusual one (*f.p.*) which is continued back from the posterior division of the muscle. (Reduced $\frac{1}{4}$.)

Fig. 5. *Platycercus eximius.* Ventral view after removal of the skin. On the left, one-half of the lower jaw has been removed. (Magnified $1\frac{1}{2}$.)

Fig. 6. *Ptistes erythropterus.* As in fig. 10, except that the thyrohyoideus is not hidden. (Magnified $1\frac{1}{2}$.)

Fig. 7. *Palæornis torquata.* Dorsal view, after removal of the membrane of the tongue. The trachea and larynx have been turned over to the right, and only sufficient of the stylohyoideus and sternohyoideus represented to show their insertions. The geniohyoideus has been removed upon the right. (Magnified $1\frac{1}{2}$.)

Fig. 8. *Pezoporus formosus.* Dorsal view, with the trachea and most of the muscles *in situ*. On the left, the sternohyoideus, stylohyoideus, and serpihyoideus have been removed, and the thyroglossus cut through near its insertion and reflected outwards, in order to reveal the thyrohyoideus and ceratoglossus superior. The posterior mylohyoideus has been represented on the right, in order to especially indicate the very slender insertion of the stylohyoideus and the contracted origin of the inner portion of the serpihyoideus. The geniohyoideus has been removed upon both sides. (Magnified $2\frac{1}{4}$.)

Fig. 9. *Conurus jendaya.* Dorsal view, after removal of the membrane of the tongue. The trachea has been turned over to the right and the geniohyoideus of either side removed; on the right the sternohyoideus and posterior mylohyoideus have also been removed. On the left only enough of the stylohyoideus has been left to show its insertion, and the serpihyoideus has been removed. (Magnified $1\frac{1}{2}$.)

Fig. 10. *Pœocephalus rüppelli.* Dorsal view, with the muscles and trachea *in situ*, and only sufficient of the stylohyoideus represented to show its insertion. The thyrohyoideus is hidden beneath the thyroglossus. (Magnified $2\frac{1}{3}$.)

Fig. 11. *Platycercus eximius.* As in fig. 17, except that the mesoglossus is not cut and the origin of the thyroglossus is intact. (Magnified 2.)

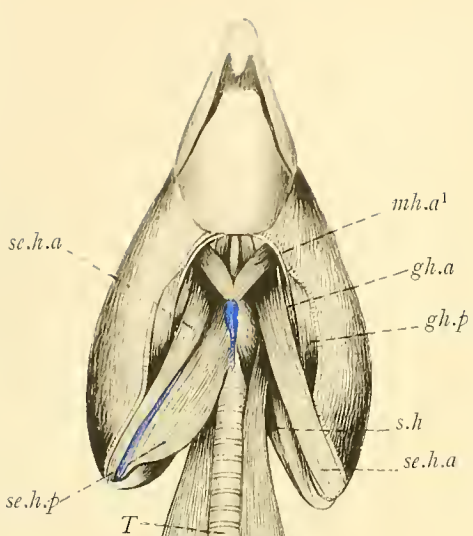


Fig. 1

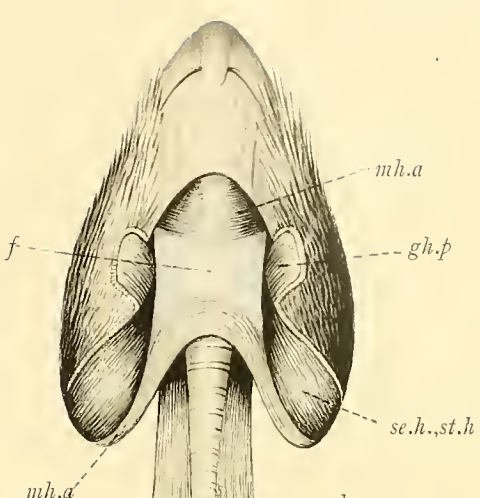


Fig. 2

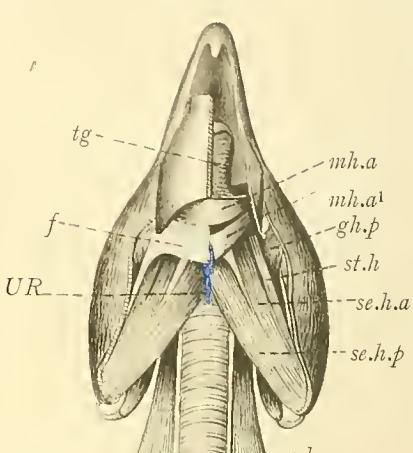


Fig. 3

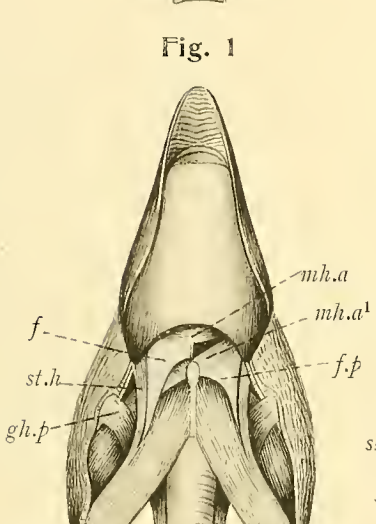


Fig. 4

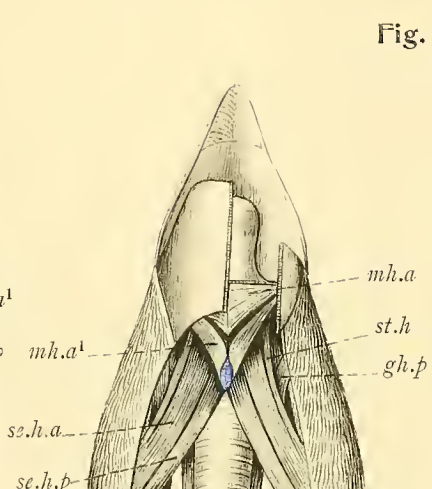


Fig. 5

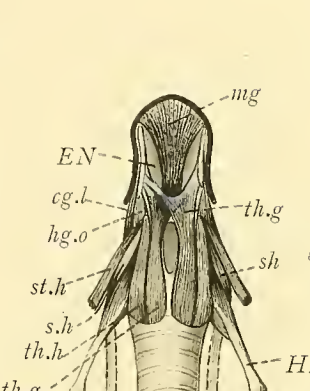


Fig. 6

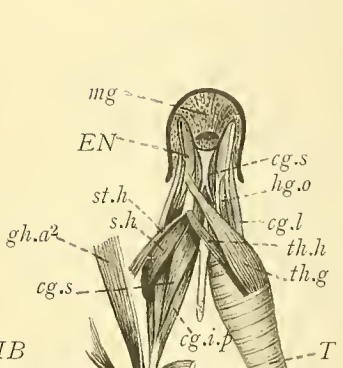


Fig. 7

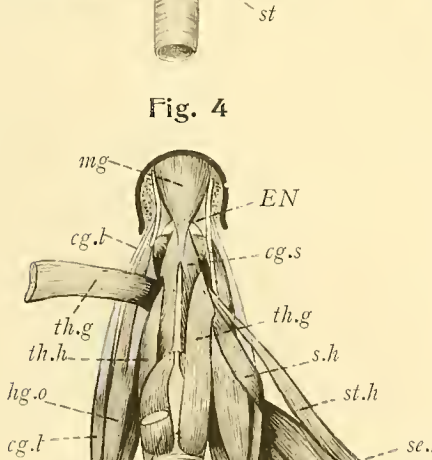


Fig. 8

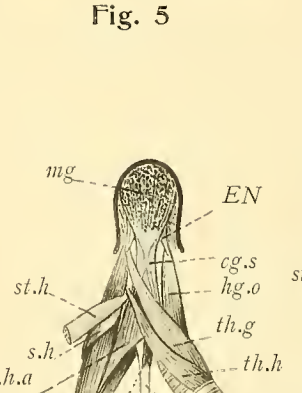


Fig. 9

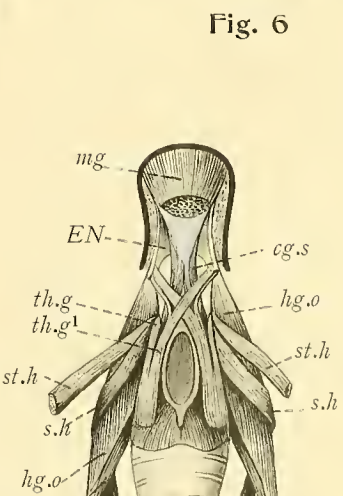


Fig. 10

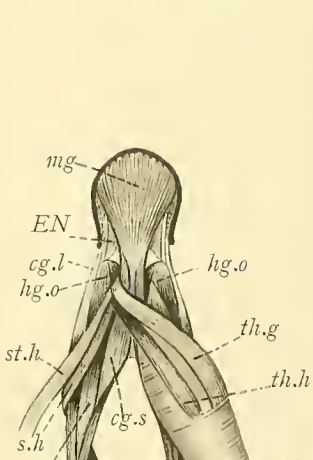


Fig. 11

H. Grönvold. del.

MYOLOGY OF THE TONGUE OF PARROTS.

Photoprint by Bale & Danielsson

PLATE XXVII.

PLATE XXVII.

Fig. 12. *Chrysotis ochrocephala.* Dorsal view. The trachea has been turned over to the right in order to show the origins and insertions of the thyrohyoideus and thyroglossus, the latter of which has no real origin, but lies free in the middle line above the basihyal. On the left only a portion of the stylohyoideus has been represented sufficient to show its insertion and general course. The geniohyoideus and sternohyoideus have been removed upon the right. (Magnified $1\frac{1}{2}$.)

Fig. 13. *Cacatua galerita.* Dorsal view, with the trachea turned over to the right and only sufficient of the stylohyoideus represented upon the left to show its insertion. The geniohyoideus has been removed upon both sides. (Magnified $1\frac{1}{2}$.)

Fig. 14. *Chrysotis panamensis.* Dorsal view. The trachea has been turned over to the right in order to show the origins and insertions of the thyrohyoideus and thyroglossus, and the peculiar connection of the latter with the sternohyoideus. Only sufficient of the stylohyoideus has been left to show its insertion. The genioglossus has been removed upon both sides. (Magnified $1\frac{1}{2}$.)

Fig. 15. *Psittacus erithacus.* Dorsal view, but with the trachea turned over to the right, and with the thyroglossus dissected away from its origin, in order to reveal the thyrohyoideus. Upon the left, but not upon the right, the full extent of the posterior mylohyoideus and sternohyoideus has been represented. The geniohyoideus has been removed upon both sides. (Magnified $1\frac{1}{2}$.)

Fig. 16. *Psittacus erithacus.* Dorsal view, with the muscles and trachea *in situ.* (Magnified $1\frac{1}{2}$.)

Fig. 17. *Coracopsis vasa.* Dorsal view, with the trachea reflected to the right and the origin of the thyroglossus cut through and turned back in order to reveal the thyrohyoideus. A portion of the mesoglossus muscle has been cut away in order to indicate the mode of termination of the ceratoglossus superior in its sheath. On the left only sufficient of the stylohyoideus has been represented to show its insertion. (Reduced $\frac{1}{4}$.)

Fig. 18. *Stringops habroptilus.* Dorsal view. The trachea and larynx have been turned over to the right and the thyroglossus partially dissected away from its insertion and raised up, in order to reveal the thyrohyoideus. On the right the serpihyoideus and the greater part of the stylohyoideus and the sternohyoideus have been removed. The geniohyoideus has been similarly removed upon both sides. (Magnified $1\frac{1}{6}$.)

Fig. 19. *Pyrrhura leucotis.* Dorsal view. The trachea has been turned over to the left and only sufficient of the stylohyoideus represented upon the right to show its insertion. The geniohyoideus has been removed upon both sides. (Magnified $1\frac{1}{2}$.)

Fig. 20. *Ara macao.* Dorsal view. The trachea has been turned over to the right and a portion of the membrane of the tongue left, in order to show the partial insertion of the thyroglossus to it. The stylohyoideus and geniohyoideus have been removed upon both sides. (Reduced $\frac{1}{4}$.)

Fig. 21. *Lorius domicella.* Dorsal view, after removal of the trachea, thyroid, and membrane of the tongue. The muscles have been dissected out and pulled slightly apart in order to show their relations to the hyoid bone. On the left the thyroglossus, thyrohyoideus, and sternohyoideus have been removed; and on the right the lateral ceratoglossal, hypoglossus obliquus, and geniohyoideus. On the right also the thyroglossus and thyrohyoideus have been cut through and enough left to show their origin from the parahyal arch. (Magnified $1\frac{1}{2}$.)

Fig. 22. *Nestor notabilis.* Dorsal view after extraction from the head and removal of the membrane of the tongue. The trachea and thyroid have been turned over towards the right to show the insertions of the thyroglossus, thyrohyoideus, and thyrohyoideus accessorius. The genioglossus has been removed upon both sides. (Reduced $\frac{1}{4}$.)

Fig. 23. *Loriculus galgulus.* Dorsal view after removal of the membrane of the tongue. The trachea has been reflected to the right in order to show the origins and insertions of the thyroglossus and thyrohyoideus. On the right, only sufficient of the stylohyoideus has been represented to show its insertion. The serpihyoideus and geniohyoideus are not represented on either side. (Magnified 2.)

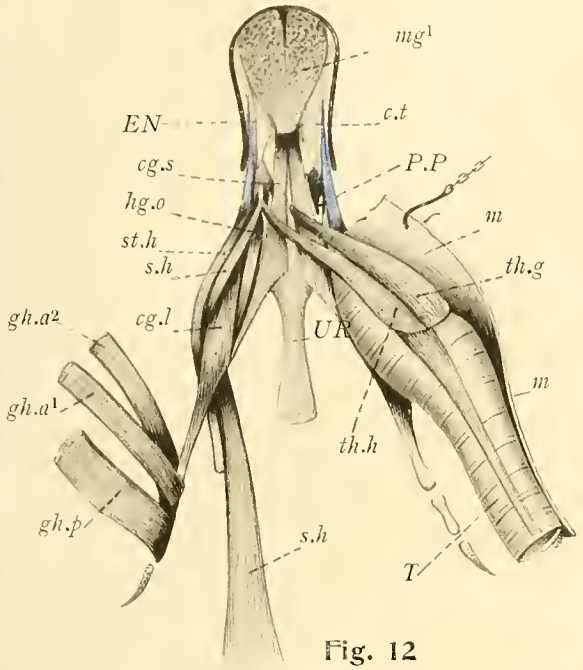


Fig. 12

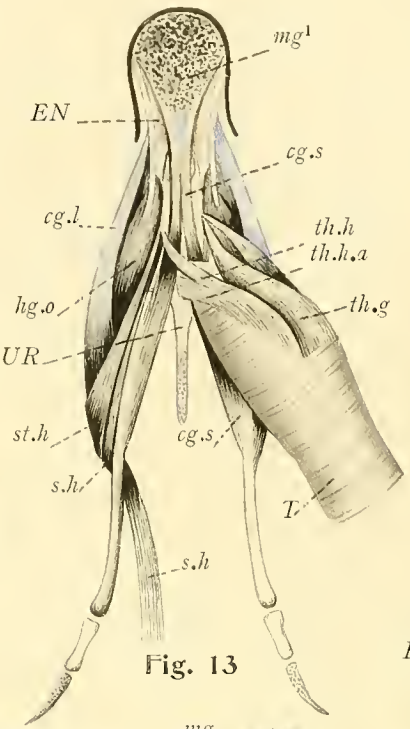


Fig. 13

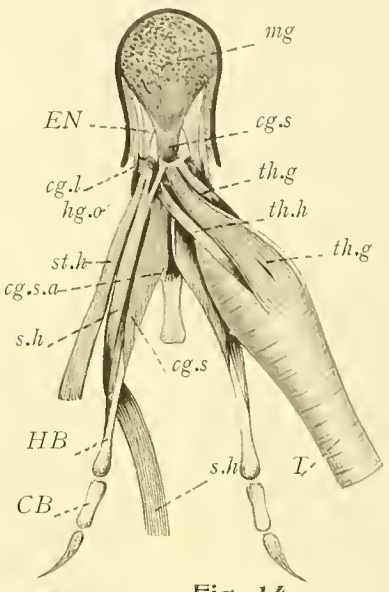


Fig. 14

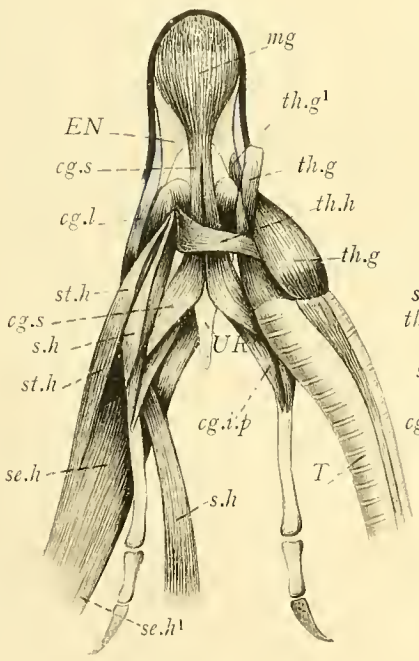


Fig. 15

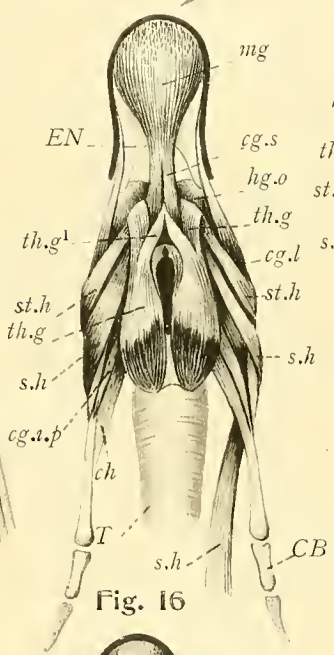


Fig. 16

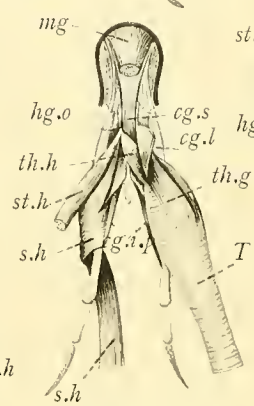


Fig. 17

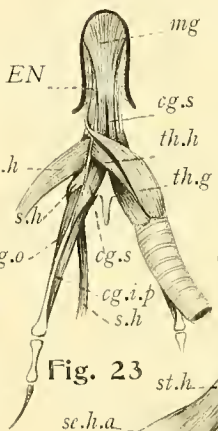


Fig. 23

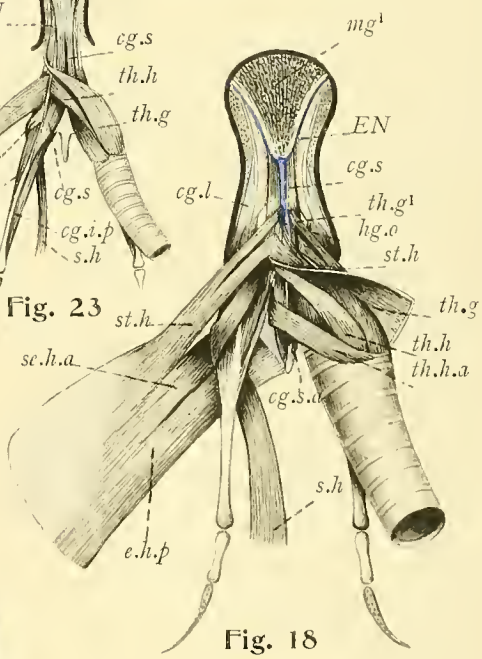


Fig. 18

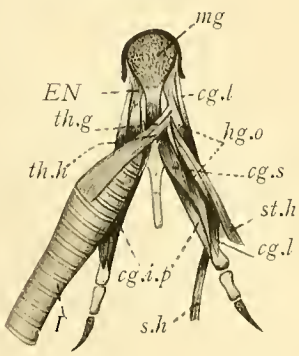


Fig. 19

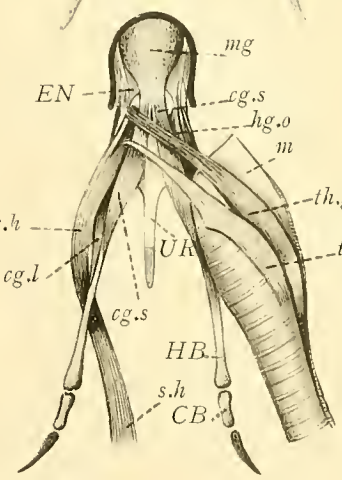


Fig. 20

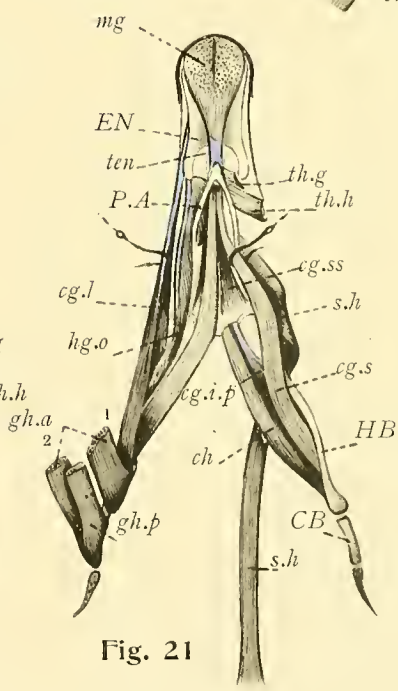


Fig. 21

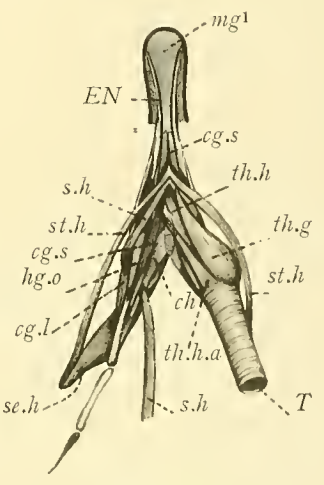


Fig. 22

PLATE XXVIII.

PLATE XXVIII.

Fig. 24. *Ara ararauna.* Ventral view after extraction from the head and removal of the anterior mylohyoideus. On the right, the posterior mylohyoideus (serpi- and stylohyoideus) and sternohyoideus have been removed; the geniohyoideus has been similarly removed upon the left. (Reduced $\frac{1}{4}$.)

Fig. 25. *Cacatua galerita.* Ventral view of the hyoid apparatus after extraction from the head. On the right, the serpihyoideus, stylohyoideus, and ceratohyoideus have been removed, and the uro-hypobranchial tendon and ceratoglossus inferior accessorius have been reflected to one side. The sternohyoideus has been removed from both sides. (Magnified $1\frac{1}{2}$.)

Fig. 26. *Stringops habroptilus.* Ventral view of the hyoid apparatus after removal from the head. On the right, the serpihyoideus, stylohyoideus, ceratoglossus inferior accessorius, uro-hypobranchial tendon, and ceratohyoideus have been removed. The sternohyoideus and geniohyoideus have been removed from both sides. (Magnified $1\frac{1}{8}$.)

Fig. 27. *Ara macao.* Ventral view, after removal of the mylohyoideus anterior. On the left, the ceratohyoideus and posterior mylohyoideus have been removed, and the uro-hypobranchial tendon and ceratoglossus inferior anticus accessorius have been reflected to the left. Upon both sides the sternohyoideus has been removed. (Reduced $\frac{1}{4}$.)

Fig. 28. *Chrysotis ochrocephala.* Ventral view of the hyoid apparatus after extraction from the head and removal of the anterior mylohyoideus. On the left, the posterior mylohyoideus has been removed, the ceratoglossus inferior anticus accessorius turned forwards, and the ceratohyoideus partially dissected away, in order to reveal the ceratoglossus inferior posticus. The sternohyoideus and geniohyoideus have been removed from both sides. (Magnified $1\frac{1}{2}$.)

Fig. 29. *Psittacus erithacus.* Ventral view of the hyoid apparatus after extraction from the head and removal of the anterior and posterior mylohyoideus. On the left, the ceratohyoideus, sternohyoideus, and geniohyoideus have been removed, and the uro-hypobranchial tendon and ceratoglossus inferior anticus accessorius have been reflected. On the right, the ceratohyoideus, ceratoglossus inferior anticus and posticus, ceratoglossus lateralis, and sternohyoideus have been removed, in order to show the relation of the hypoglossus obliquus to the basihyal and hypobranchial. (Magnified $1\frac{1}{2}$.)

Fig. 30. *Conurus cactorum.* Ventral view after removal of the anterior mylohyoideus. On the right, the posterior mylohyoideus and ceratohyoideus have been removed, and the uro-hypobranchial tendon and ceratoglossus inferior accessorius reflected to one side. The geniohyoideus and sternohyoideus have been similarly removed upon both sides. (Magnified $1\frac{1}{2}$.)

Fig. 31. *Coracopsis vasa.* Ventral view, after removal of the anterior mylohyoideus. On the right, the posterior mylohyoideus (serpi- and stylohyoideus) and ceratohyoideus have been removed, and the uro-hypobranchial tendon and ceratoglossus inferior anticus accessorius have been reflected. (Reduced $\frac{1}{3}$.)

Fig. 32. *Palæornis torquata.* Ventral view. On the right, the posterior mylohyoideus and sternohyoideus have been removed, and the uro-hypobranchial tendon and ceratoglossus inferior accessorius have been reflected to the right. The geniohyoideus has been removed from both sides. (Magnified $1\frac{1}{2}$.)

Fig. 33. *Brotogerys pyrrhopterus.* Ventral view. On the left, the posterior mylohyoideus, ceratohyoideus, and sternohyoideus have been removed, and the uro-hypobranchial tendon and ceratoglossus inferior accessorius have been reflected. On the right, the ceratohyoideus has been left *in situ*, and the ceratoglossus inferior accessorius and uro-hypobranchial tendon are undisturbed. The geniohyoideus and anterior mylohyoideus have been removed from both sides. (Magnified $1\frac{1}{2}$.)

Fig. 34. *Psittinus incertus.* Ventral view. On the left, the posterior mylohyoideus, uro-hypobranchial tendon, ceratoglossus inferior accessorius, and ceratohyoideus have been removed in order to show the ceratoglossus inferior posticus. Upon both sides the sternohyoideus, anterior mylohyoideus, and geniohyoideus have been removed. (Magnified $1\frac{1}{2}$.)

Fig. 35. *Ptistes erythropterus.* Ventral view of the hyoid apparatus after removal from the head. On the left, the posterior mylohyoideus, ceratohyoideus, uro-hypobranchial tendon, and the ceratoglossus inferior accessorius have been removed. The geniohyoideus and sternohyoideus have been similarly removed from both sides. (Magnified $1\frac{1}{2}$.)

Fig. 36. *Conurus jendaya.* Ventral view after extraction from the head and removal of the anterior mylohyoideus. On the left, the posterior mylohyoideus and ceratohyoideus have been removed, and the ceratoglossus inferior accessorius and uro-hypobranchial tendon have been reflected to one side. Upon both sides the sternohyoideus and geniohyoideus have been removed. (Magnified $1\frac{1}{2}$.)

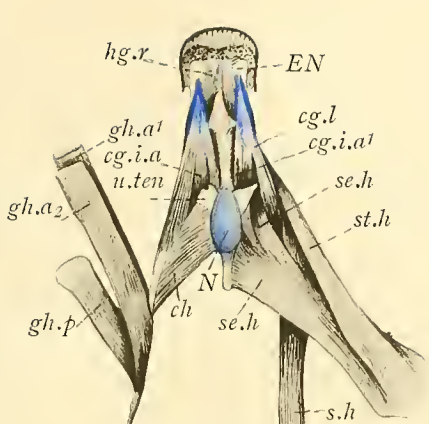


Fig. 24

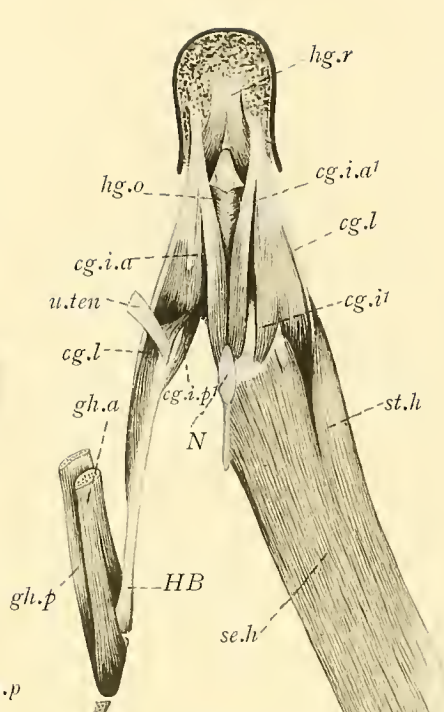


Fig. 25

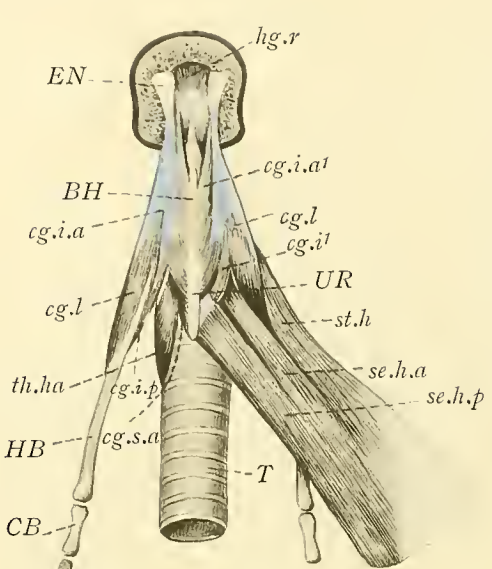


Fig. 26

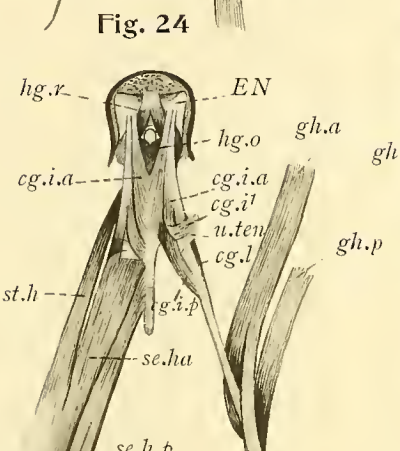


Fig. 27

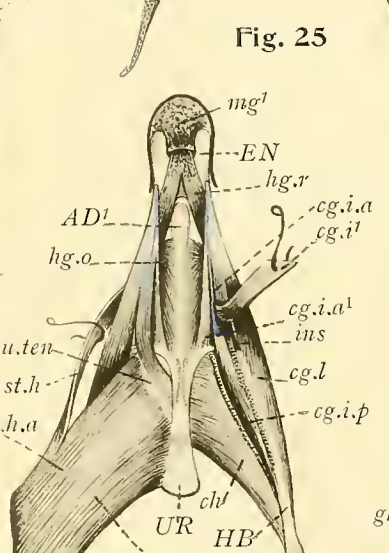


Fig. 28

Fig. 31

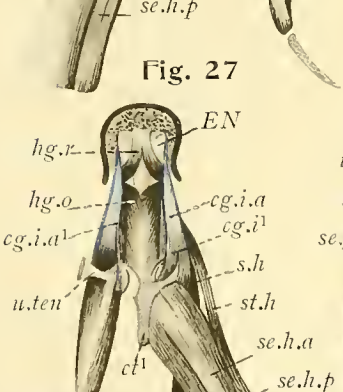


Fig. 32

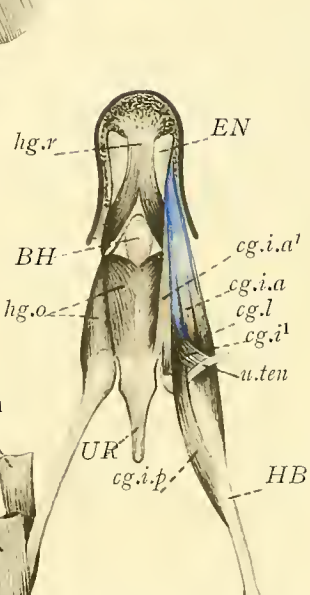


Fig. 29

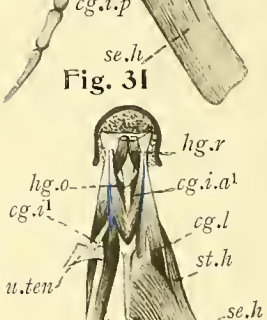


Fig. 30

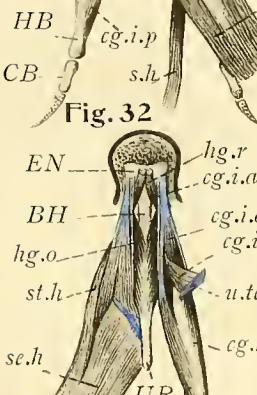


Fig. 36

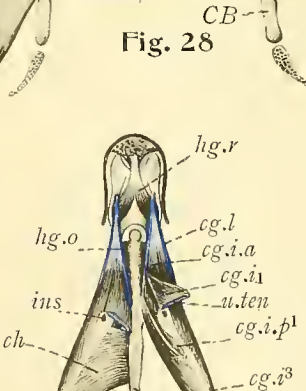


Fig. 33

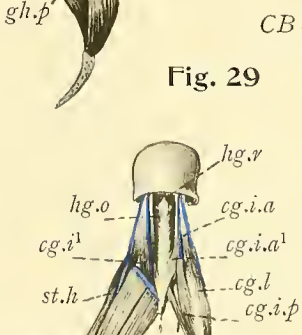


Fig. 34

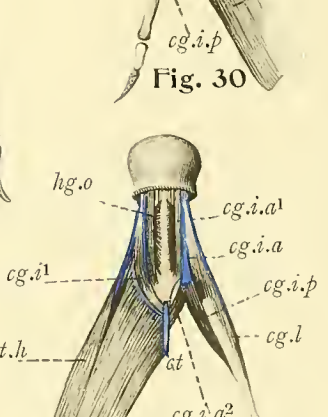


Fig. 35

PLATE XXIX.

PLATE XXIX.

Fig. 37. *Lorius domicella.* Hyoid apparatus removed from the head and its muscles dissected from the ventral aspect to show their relations to the various portions of the hyoid bone. The anterior and posterior mylohyoideus and the geniohyoideus have been removed. On the left side the ceratohyoideus, hypoglossus obliquus, and rectus have been dissected off, and on the right the lateral and inferior ceratoglossals were similarly removed. (Magnified $1\frac{1}{2}$.)

Fig. 38. *Lorius flavo-palliatus.* Ventral view of the hyoid apparatus after removal from the head. On the right the lateral and inferior ceratoglossals have been removed, and on the left the membrane of the apical portion of the tongue and the ceratohyoideus. The anterior and posterior mylohyoideus, geniohyoideus, and serpihyoideus have been dissected off. (Magnified $1\frac{1}{2}$.)

Fig. 39. *Eos riciniata.* Ventral view after removal from the head. The anterior and posterior mylohyoideus (serpihyoideus and stylohyoideus) and sternohyoideus have been removed, and on the right the ceratohyoideus and geniohyoideus also. (Magnified $1\frac{1}{2}$.)

Fig. 40. *Pyrrhura leucotis.* Ventral view. On the right the serpihyoideus, stylohyoideus, and sternohyoideus have been removed, and the uro-hypobranchial tendon and ceratoglossus inferior accessorius reflected to the right. The geniohyoideus has been removed upon both sides. (Magnified $1\frac{1}{2}$.)

Fig. 41. *Psittacula passerina.* Ventral view. On the right, the posterior mylohyoideus, uro-hypobranchial tendon, ceratoglossus inferior accessorius, and ceratoglossus inferior accessorius secundus have been removed. The sternohyoideus and geniohyoideus have been similarly removed upon both sides. (Magnified $2\frac{1}{2}$ nearly.)

Fig. 42. *Loriculus galgulus.* Ventral view. On the right, the posterior mylohyoideus, sternohyoideus, and ceratoglossus inferior accessorius have been removed. (Magnified 2.)

Fig. 43. *Pionopsittacus pileatus.* Ventral view. On the left, the posterior mylohyoideus, the ceratoglossus inferior anticus, and the uro-hypobranchial tendon have been removed. The geniohyoideus and genioglossus have been removed upon both sides. (Magnified $1\frac{1}{2}$.)

Fig. 44. *Platycercus eximius.* Ventral view. On the right, the serpihyoideus and stylohyoideus have been removed, and the uro-hypobranchial tendon has been cut through at its inner attachment, and together with the ceratoglossus inferior accessorius reflected to the right. Upon both sides the geniohyoideus and sternohyoideus have been removed. (Magnified $1\frac{1}{2}$.)

Fig. 45. *Bolborhynchus lineolatus.* Ventral view. On the left, the serpihyoideus, stylohyoideus, sternohyoideus, and geniohyoideus have been removed. The two latter muscles have also been removed on the right. (Magnified $1\frac{1}{2}$.)

Fig. 46. *Nestor notabilis.* Ventral view of the hyoid muscles after removal from the head. On the right, the posterior mylohyoideus, sternohyoideus, and uro-hypobranchial tendon have been removed. (Reduced $\frac{1}{4}$.)

Fig. 47. *Pezoporus formosus.* Ventral view after removal of the hyoid apparatus from the head. On the left, the posterior mylohyoideus and the ceratoglossus inferior accessorius have been removed, and the sternohyoideus and geniohyoideus have been similarly removed upon both sides. (Magnified 2.)

Fig. 48. *Nasiterna pusio.* Ventral view after extraction from the head and removal of the anterior and posterior mylohyoideus. On the left, the ceratohyoideus, sternohyoideus, ceratoglossus inferior anticus and posticus, and ceratoglossus lateralis have been removed in order to show the hypoglossus obliquus. On the right, the ceratohyoideus and sternohyoideus have been removed. Upon both sides the geniohyoideus has been dissected away. (Four times nat. size.)

Fig. 49. *Eclectus pectoralis.* Ventral view. On the right, the serpihyoideus, stylohyoideus, ceratohyoideus, and sternohyoideus have been removed, and the uro-hypobranchial tendon and ceratoglossus inferior accessorius have been reflected. The geniohyoideus has been removed from both sides. (Magnified $1\frac{1}{2}$.)

Fig. 50. *Lorius domicella.* Lateral aspect of the hyoid apparatus, after extraction from the head and removal of the membrane of the tongue. The relation of the hypoglossus rectus to the mesoglossus is better seen than in any other view. (Magnified $1\frac{1}{2}$.)

Fig. 51. *Loriculus galgulus.* Ventral view. On the left, one-half of the lower bill and of the persistent fascia (*f.*) has been cut away. (Magnified $1\frac{1}{2}$.)

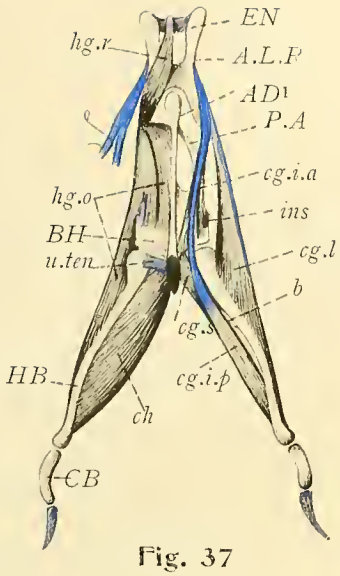


Fig. 37

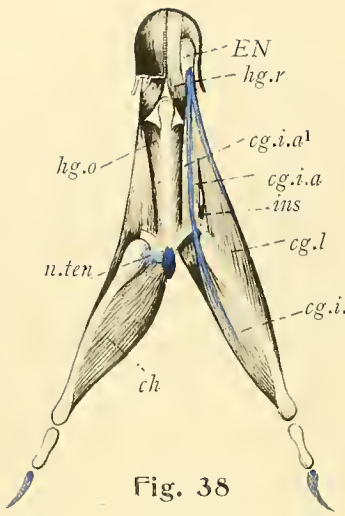


Fig. 38

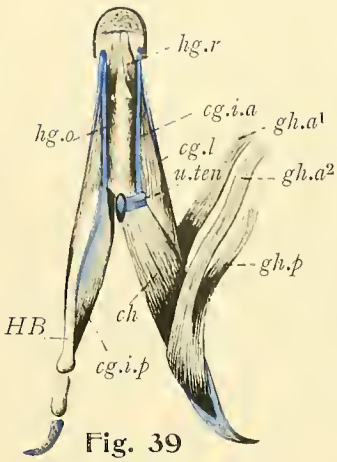


Fig. 39

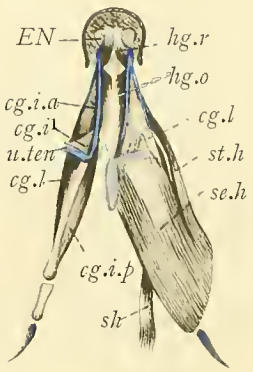


Fig. 40

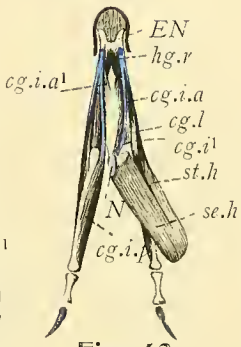


Fig. 42

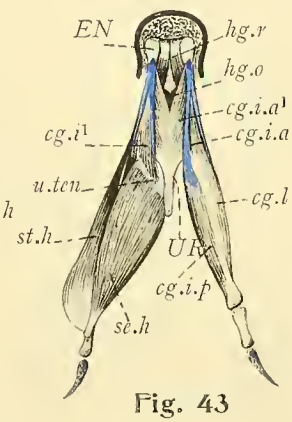


Fig. 43

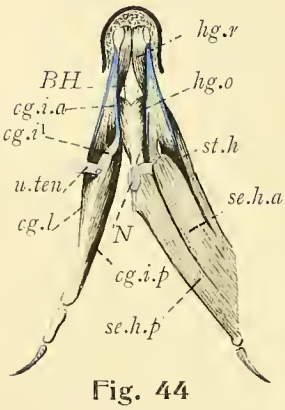


Fig. 44

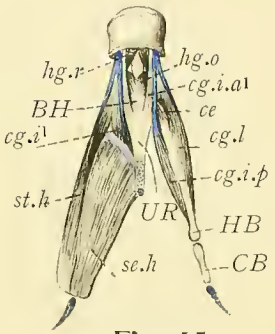


Fig. 45

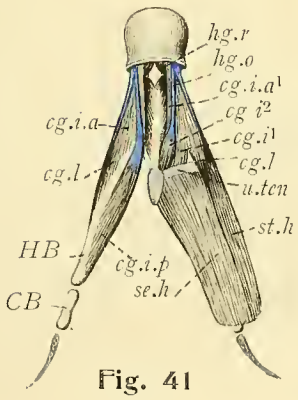


Fig. 41

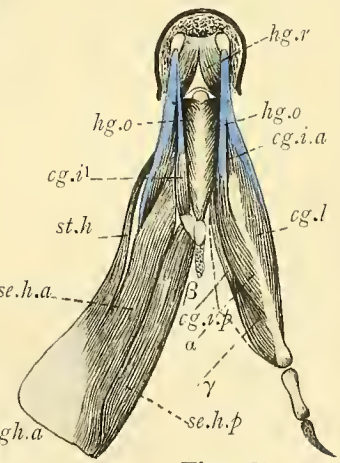


Fig. 47

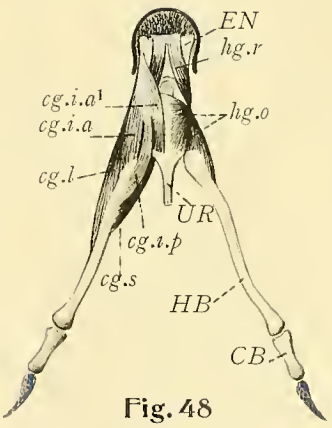


Fig. 48

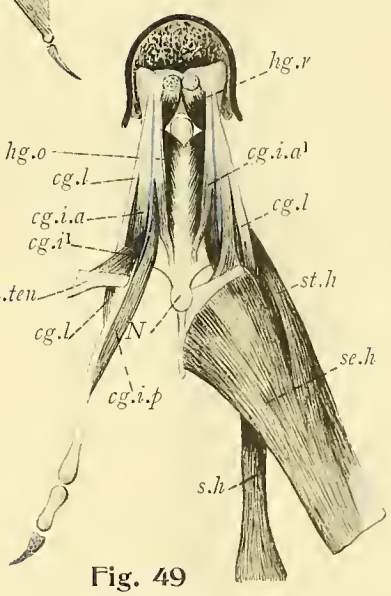


Fig. 49

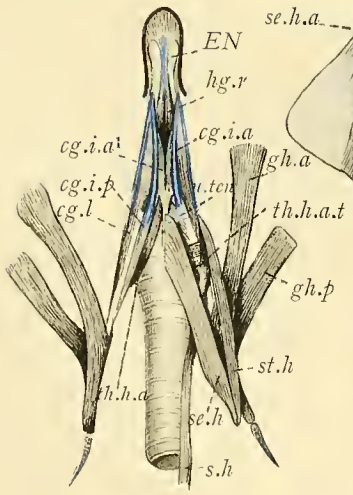


Fig. 46

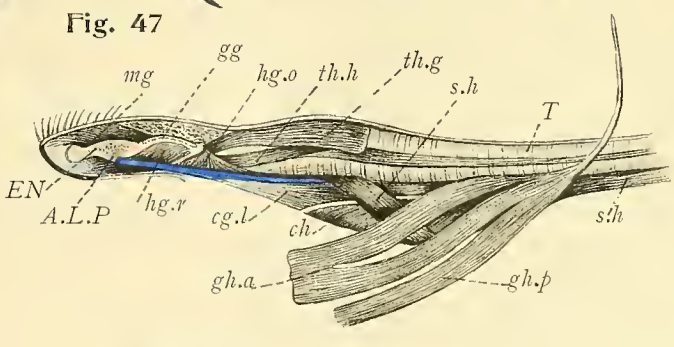


Fig. 50

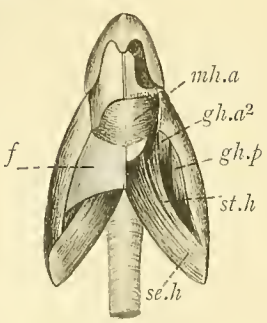


Fig. 51

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON
(continued).

	To Fellows. £ s. d.	To the Public. £ s. d.
VOLUME XIV. (1896–1898, containing 47 Plates) .	Price 5 5 0	7 0 0
Part 1. (1896, containing 2 Plates)	„ 0 6 0	0 8 0
„ 2. (1896, containing 6 Plates)	„ 0 9 0	0 12 0
„ 3. (1897, containing 9 Plates)	„ 0 15 9	1 1 0
„ 4. (1897, containing 10 Plates)	„ 1 10 0	2 0 0
„ 5. (1898, containing 2 Plates)	„ 0 6 0	0 8 0
„ 6. (1898, containing 7 Plates)	„ 0 18 0	1 4 0
„ 7. (1898, containing 6 Plates)	„ 0 11 3	0 15 0
„ 8. (1898, containing 5 Plates and Title and Index)	„ 0 9 0	0 12 0
VOLUME XV. (1898–1901, containing 52 Plates) .	Price 5 15 6	7 14 0
Part 1. (1898, containing 8 Plates)	„ 0 15 9	1 1 0
„ 2. (1899, containing 5 Plates)	„ 0 9 0	0 12 0
„ 3. (1899, containing 4 Plates)	„ 0 9 0	0 12 0
„ 4. (1899, containing 4 Plates)	„ 0 9 0	0 12 0
„ 5. (1900, containing 24 Plates)	„ 2 12 6	3 10 0
„ 6. (1901, containing 4 Plates)	„ 0 11 3	0 15 0
„ 7. (1901, containing 3 Plates and Title and Index)	„ 0 9 0	0 12 0
VOLUME XVI.		
Part 1. (1901, containing 6 Plates)	Price 0 18 0	1 4 0
„ 2. (1901, containing 5 Plates)	„ 0 11 3	0 15 0
„ 3. (1901, containing 9 Plates)	„ 0 15 9	1 1 0
„ 4. (1902, containing 5 Plates)	„ 0 9 0	0 12 0
„ 5. (1902, containing 4 Plates)	„ 0 13 6	0 18 0
„ 6. (1902, containing 3 Plates)	„ 0 15 9	1 1 0
„ 7. (1902, containing 3 Plates)	„ 0 11 3	0 15 0

CONTENTS.

VI. *On the Myology of the Tongue of Parrots, with a Classification of the Order, based upon the Structure of the Tongue.* *By* GEORGE P. MUDGE, *A.R.C.S. Lond., F.Z.S., Lecturer on Biology, London School of Medicine for Women, and Demonstrator of Biology, London Hospital Medical School.* (Plates XXVI.–XXIX.) page 211

THE PUBLICATIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

THE scientific publications of the Zoological Society of London are of two kinds—"Proceedings," published in an octavo form, and "Transactions," in quarto.

According to the present arrangements, the "Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the "Proceedings" by the Committee of Publication. A large number of coloured plates and engravings are attached to each annual volume of the "Proceedings," to illustrate the new or otherwise remarkable species of animals described in them. Among such illustrations, figures of the new or rare species acquired in a living state for the Society's Gardens are often given.

The "Proceedings" for each year are issued in four parts, on the first of the months of June, August, October, and April, the part published in April completing the volume for the last half of the preceding year. Commencing from January 1901 they form two half-yearly volumes.

The "Transactions" contain such of the more important communications made to the scientific meetings of the Society as, on account of the nature of the plates required to illustrate them, are better adapted for publication in the quarto form. They are issued at irregular intervals.

Fellows and Corresponding Members, upon payment of a Subscription of £1 1*s.* before the day of the Anniversary Meeting in each year, are entitled to receive all the Society's Publications for the year. They are likewise entitled to purchase the Publications of the Society at 25 per cent. less than the price charged for them to the Public. A further reduction of 25 per cent. is made upon purchases of Publications issued prior to 1871, if they exceed the value of five pounds.

Fellows also have the privilege of subscribing to the Annual Volume of the 'Zoological Record' for a sum of £1 (which includes delivery in the United Kingdom *only*), but this privilege only holds good if the subscription is paid before the First of December in each year.

Such of these publications as are in stock may be obtained at the Society's Office (3 Hanover Square, W.), at Messrs. Longmans', the Society's publishers (Paternoster Row, E.C.), or through any bookseller.

October, 1902.

P. L. SCLATER,
Secretary.

TRANSACTIONS

OF

THE ZOOLOGICAL SOCIETY

OF LONDON.

VOL. XVI.—PART 6.

LONDON:

PRINTED FOR THE SOCIETY,

SOLD AT THEIR HOUSE IN HANOVER-SQUARE;

AND BY MESSRS. LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

August 1902.

Price 21*s.*

Smithsonian Institution
SEP 23 1902
National Museum

Taylor and Francis, Printers.] [Red Lion Court, Fleet Street.

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

		To Fellows. £	s.	d.	To the Public. £	s.	d.
VOLUME I. (1833–1835, containing 59 Plates) . .	Price	3	13	6	4	18	0*
VOLUME II. (1835–1841, containing 71 Plates) . .	„	4	0	0	5	6	6*
VOLUME III. (1842–1849, containing 63 Plates) . .	„	3	8	3	4	11	0*
VOLUME IV. (1851–1862, containing 77 Plates) . .	„	6	2	0	8	2	6†
VOLUME V. (1862–1866, containing 67 Plates) . .	„	5	4	3	6	19	0†
VOLUME VI. (1866–1869, containing 92 Plates) . .	„	11	5	0	15	0	0†
VOLUME VII. (1869–1872, containing 73 Plates) . .	„	10	4	0	13	12	0†
VOLUME VIII. (1872–1874, containing 82 Plates) . .	„	9	8	3	12	11	0†
VOLUME IX. (1875–1877, containing 99 Plates) . .	„	12	1	6	16	2	0†
VOLUME X. (1877–1879, containing 95 Plates) . .	„	10	0	3	13	7	0†
GENERAL INDEX, Vols. I. to X. (1833–1879) .	„	0	7	6	0	10	0
VOLUME XI. (1880–1885, containing 97 Plates) . .	„	9	12	0	12	16	0
VOLUME XII. (1886–1890, containing 65 Plates) . .	„	5	8	0	7	4	0
VOLUME XIII. (1891–1895, containing 62 Plates) . .	„	6	8	3	8	11	0

* No copies of these volumes remain in stock.

† Only complete copies of these volumes are left in stock.

Continued on page 3 of Wrapper.

VII. *On* Okapia, *a new Genus of* Giraffidæ, *from Central Africa.*

By E. Ray Lankester, *M.A., LL.D., F.R.S., F.Z.S., Director of the Natural History Departments of the British Museum, Correspondent of the Institute of France.*

Received and read November 19, 1901.

[Plates XXX.–XXXII.]

Contents.

		Page
I.	History of the Discovery of the Okapi	279
II.	The Region inhabited by the Okapi	282
III.	Description of the Skull and Lower Jaw of the Okapi	283
IV.	The Areas of Tumescence of the Giraffine Skull and the Nature and Origin of the Horns of Pecora	291
V.	Characters presented by the Skin of the Okapi	300
VI.	Characters of the Genus *Okapia* and of the Species *O. johnstoni*	302
VII.	Appendix	304
VIII.	Explanation of the Plates	309

I.—History of the Discovery of the Okapi.

The animal to which this memoir relates is, we are told by Sir Harry Johnston, who obtained the skin and skulls here described and presented them to the British Museum, known to the natives in the neighbourhood of the Semliki Forest by the name "Okapi."

The following passage in Sir Henry Stanley's 'In Darkest Africa,' vol. ii. p. 442, first drew Sir Harry Johnston's attention to the animal. Stanley says, in reporting on the language of the Congo dwarfs whom he saw in 1888:—"The Wambutti (these dwarfs) knew a donkey and called it 'Atti.' They say that they sometimes catch them in pits. What they can find to eat is a wonder. They eat leaves." From conversation with Sir Henry Stanley during the present year (1901), Sir Harry Johnston has come to the conclusion that Stanley and his companions occasionally caught sight of the Okapi when they traversed the region of the Congo forest on the western side of the Semliki River. His own acquaintance with the animal, which he was led to seek by Stanley's brief reference to it as a donkey, is given in the following extracts from a letter to me dated November 1901. The word "Atti" given by Stanley is apparently a variant of the name "Okapi," which Sir Harry Johnston found to be the name for it used by his informants:—

"Somewhere about March 1900 I first heard of the Okapi from the Congo dwarfs who were staying with me at Entebbe, Uganda. At the beginning of July I reached the Semliki Forest, in the Congo Free State. The first Belgian official who confirmed the Okapi stories, and who assisted me to get the bandoliers of skin, was a Lieutenant Meura.

Lieutenant Meura knew a good deal about the Okapi, though he still believed it to be a kind of horse. Unfortunately he died soon afterwards of black-water fever. His second in command at Fort Mbeni, on the border of the Semliki Forest, was Karl Eriksson, who had been a non-commissioned officer in the Swedish Army and had become an officer in the service of the Congo Free State. After my fruitless search through the nearer parts of the Semliki Forest, in which I only got one more strip of skin from a native, I was obliged to leave the forest owing to the absolute collapse of my caravan, all the Negro porters having gone down with violent forms of fever. So completely collapsed were they, in fact, that the Belgians had to turn out all their soldiers and station-labourers to carry my loads back to British territory. To console me for my disappointment, Meura promised to use his best endeavours to get a complete skin. After his death, which took place soon afterwards, Eriksson most generously carried out that promise. I must have sent home the bandoliers to Sclater in October 1900, as I was a long while getting back to my headquarters.

"The complete skin sent by Eriksson was probably despatched from the Congo Free State about February 1901, and arrived in Entebbe in March, reaching me at the end of that month at the Eldama Ravine, in the eastern part of the Protectorate. In the original note (which, unfortunately, I cannot at this moment find) that Eriksson sent accompanying the skin he refers distinctly to the hoofs as though they were on the skin, describing them as bluish black and like those of an antelope, his point being, of course, his surprise at discovering the creature not to be a soliped but cloven-hoofed. When Jackson opened the skin at Entebbe the horny hoofs had apparently disappeared. At first we thought that they had been eaten by rats, but Doggett (my taxidermist) suggests that they simply fell off the bones. In other cases we found it constantly happened, after the foot of a hoofed mammal had become dry, that the horny sheath fell off the bone. When the skin reached me the lower jaw of the bigger skull was still attached to it. Eriksson also in his letter said, 'I send you a skin and skull of the Okapi,' &c., and a little later on, 'also another skull.' As the bigger skull supposed to belong to the skin exactly fits the mandible which actually was attached to the skin when it reached me, I assume that the larger of the two skulls belongs to the skin. That is all I know with regard to this mysterious animal. After I left the Congo Free State I discussed this question with natives of the little territory of Mboga, which happens to be British, and is actually part of the Semliki Forest. They all knew the creature, and declared that it was fairly common in their country. Nevertheless, although these people have brought us in young elephants, chimpanzees, and all sorts of other creatures, they have failed hitherto to bring another specimen of the Okapi."

The strips of skin referred to in this letter as "bandoliers" were covered with hair, coloured dark brown and white in alternate bands. They were received in London in November 1900, and were exhibited by Dr. Sclater at the Meeting of this Society on December 18th (see P. Z. S. 1900, p. 950). They were again exhibited and

Text-fig. 1.

Bandoliers made from the skin of the Okapi.
(From P. Z. S. 1901, i. p. 51.)

described at this Society's Meeting on Feb. 5th, 1901, as indicating a new Zebra, to which Dr. Sclater gave the name "*Equus johnstoni*." The figure of these "bandoliers" published by Dr. Sclater is here reproduced (text-fig. 1).

The complete skin, which arrived in London in July 1901 and is now mounted in the gallery of the Natural History Museum (as represented in Plate XXX.), shows that the striping of the pelt extends over a very limited area, being confined to the haunches and the fore and hind legs above the carpus and tarsus respectively. The "bandoliers" in question are found, on comparison with the complete skin, to have been cut from the haunches, and their exact position can be traced. A comparison leaves no doubt that these strips of skin belonged to the Okapi, and therefore the specific name "*johnstoni*" given by Dr. Sclater will remain as the designation of the Okapi. At the same time, the close study of the bandoliers and the complete Okapi skin render it certain that the striping on the hind legs of the Okapi is, to a small extent, variable in individuals.

It was at once apparent to Sir Harry Johnston, on receiving the complete skin with the double hoof-bones, that the Okapi is not really a horse-like animal at all, but belonged to the group of Artiodactyle Ungulates. The absence of horns and the great length of the ears account for the comparison of the animal to a donkey or a zebra frequently made by natives when describing it. But the examination of the two skulls and the lower jaw enabled Sir Harry Johnston to recognize before despatching the specimens to England that the Okapi is closely related to the Giraffes. In the letter written in April 1901, which he sent to me announcing the fact that he had packed up and sent off the skin and skulls of the Okapi from Uganda to England, Sir Harry expresses the opinion that the Okapi is a hornless kind of giraffe and possibly to be referred to Gaudry's genus *Helladotherium*[1].

As will be seen from the drawing and description of the skulls and lower jaw here given, the identification made by Sir Harry Johnston was practically correct. Though the Okapi differs in important characters of generic value from the *Helladotherium* of the Miocene of Pikermi and India, it yet stands close to it as a hornless[2] representative of that remarkable and once extensive group, the Giraffidæ, of which it and the Giraffe are the only survivors. There were many and varied genera belonging to the Giraffidæ in the Miocene period, some with larger bony outgrowths of the skull than has the recent Giraffe and some without such outgrowths.

II.—The Region inhabited by the Okapi.

Before proceeding to further description of the characters exhibited by the skin and skulls in our possession, it is well to put on record the nature of the region in which the Okapi is found. The Semliki River flows from the Albert Edward Lake to the Albert Nyanza, and it is in the forest on the western side of the river that the Okapi lives. Sir Harry Johnston estimates the area within which it certainly occurs as being as large as the Principality of Wales, and it may have a larger range. There are

[1] See also the 'Times,' May 7th, 1901.

[2] May 27th, 1902.—Now shown not to be hornless; see Appendix, p. 304.

certainly many thousand individuals of it inhabiting the forest of this region. The equatorial position of the forest renders the atmosphere extremely hot and damp, whilst overhead the foliage is so dense that little or no light penetrates to the ground. There is ample room for locomotion among the trunks of the large trees, and it is here that the Okapi roams. The Okapi is strictly a forest animal, feeding at the occasional openings in the forest where decay and storms have broken down the continuity of dark leafless avenues. The natives are extremely reluctant to penetrate far into the forest, and hence it is that the Okapi is but seldom seen and is known chiefly to the Wambutti or Akka, the dwarf race who, like the Okapi itself, seek the recesses of the forest as a protection against light-loving enemies [1].

The peculiar disposition of the striping of the Okapi's legs and body must be explained, if explained at all, by a consideration of its habits and surroundings; and at present we know no more on those matters than can be derived from the description given by travellers of the heat, moisture, gloom, and silence, as well as the enormous extent, of the Semliki and Congo forests.

III.—Description of the Skull and Lower Jaw of the Okapi.

As the form and characters of the skull are those which are important in determining the affinities of the Okapi and in characterizing the genus *Okapia*, I shall describe these before proceeding to a consideration of the skin, the features of which may, in many respects, be only of specific value. One of the two skulls sent is considerably larger than the other, and belongs to the skin, the lower jaw having been still attached to the latter when received by Sir Harry Johnston.

The skulls are figured in Plates XXXI. and XXXII., two-thirds of the natural size.

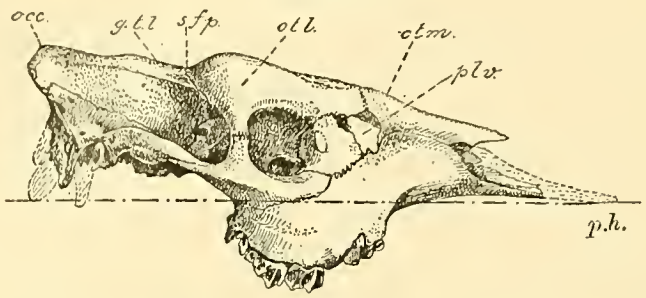
The state of the dentition of the larger skull indicates that it is that of an animal far from mature and corresponds to that of a Giraffe of two-thirds the linear measurements of an adult. This fact has an important bearing upon the conclusions we may form as to the absence of horns, especially when taken into consideration with the fact that there was no evidence in the skin as sent home as to the presence of male or female generative organs. The skull and skin may be those of an immature male or of an immature female. In Giraffes, however, of much less than two-thirds growth the lateral horn-bones ("ossicusps") are present as separately ossifying cones. And it seems probable from the fact that none of the native reports concerning the Okapi refer (according to Sir Harry Johnston) to the existence of

[1] The Okapi is not unfrequently captured in dug-out traps and speared by the natives in the neighbourhood of the Independent Congo State fort whence Sir Harry Johnston obtained it. It is not an animal which can attract the sportsman, on account of the heat and darkness of the forest where it lives; but I have no doubt that anyone who would go and stay six months or more on this spot would be able to obtain several complete specimens without firing a shot.

horns, but rather emphasize their absence by comparing the animal to a horse, that no horns are ever developed in either male or female Okapi [1].

Given an animal which, as shown by the skin, possessed no rudimentary digits by

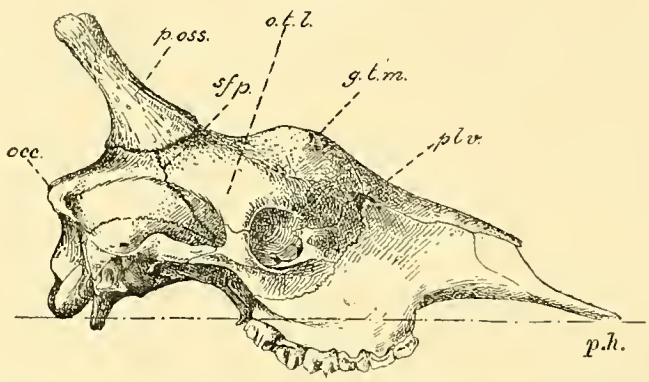
Text-fig. 2.



Lateral view of the skull of the Okapi, the individual being about two-thirds grown, to compare with the similar figure of a Giraffe's skull (text-fig. 3).

occ., occipital crest; *g.t.l.*, position of the lateral parietal tumescence and epiphysis of the Giraffe, absent here; *sfp.*, fronto-parietal suture; *otl.*, the lateral frontal tumescence of the Okapi, absent in Giraffe; *otm.*, the median basinasal tumescence of the Okapi; *plv.*, prælacrymal vacuity; *p.h.*, palatine horizontal.

Text-fig. 3.



Lateral view of the skull of a Giraffe, about two-thirds grown, to compare with the similar view of the Okapi's skull, which also appears to have belonged to an individual which had completed only two-thirds of its growth.

occ., occipital crest; *p.oss.*, parietal osseous cap (epiphysis) overlying the parietal conical upgrowth; *sfp.*, fronto-parietal suture; *o.t.l.*, position of the lateral frontal tumescence in the Okapi, absent here; *g.t.m.*, the characteristic median tumescence of the Giraffe's frontal, devoid in this specimen of any secondary cap or epiphysis, absent in the Okapi; *plv.*, the prælacrymal vacuity; *p.h.*, palatine horizontal.

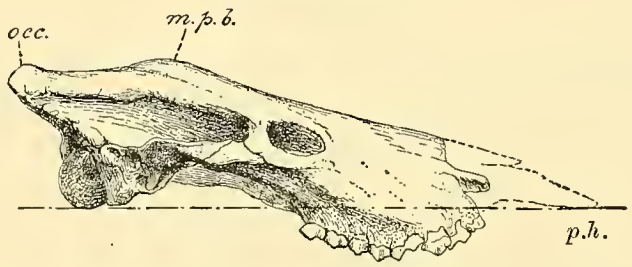
the side of the main paired hoof-bearing digits—what are the characters of the skull which in the first instance enable us to refer the specimen to the Giraffidæ? In the first place, the general characters of the dentition—absence of incisors and

[1] See Appendix and text-figure on p. 304, giving an account of two new specimens, male and female, with horns two to three inches in length.

canines in the upper jaw, the presence of brachydont selenodont molars, the group of eight anterior teeth in the lower jaw (incisors and canines), and the long diastema between these and the molars—are characters only found in the Pecora and in typical Giraffidæ (*Vellericornia*), Cervidæ (*Cervicornia*), or Bovidæ (*Cavicornia*). The absence of "pettitoes" renders Cervine and Bovine affinities improbable, whilst Antelopine and Giraffine are more likely. Antelopes without rudimentary digits are known, but are exceptional. The absence of horns would tell no more against Antelopine than Giraffine affinities, since hornless females are known among the former.

The great length of the postorbital region of the Okapi's skull (text-fig. 2, p. 284) is, however, not at all Antelopine, and is more nearly approached (though not nearly equalled) by the Giraffe. Moreover, the skull of the Okapi is not only astonishingly long in the postorbital region (see Plates XXXI. & XXXII.), but it presents a great peculiarity in the fact that this region is in the same horizontal plane as the præorbital region. In fact, the basicranial axis and the basifacial axis of the Okapi's skull appear

Text-fig. 4.



Lateral view of the skull of *Helladotherium*, from the Miocene of Pikermi: after Gaudry.

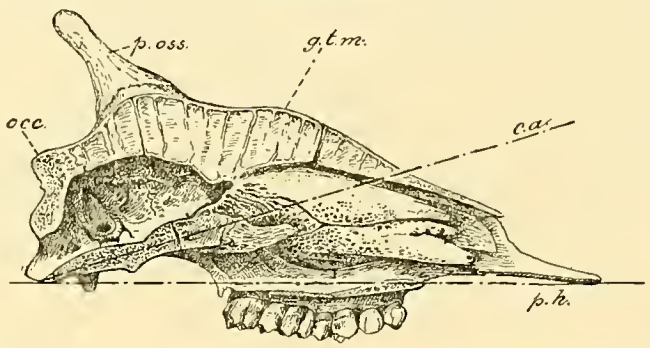
occ., occipital crest; *p.h.*, palatine horizontal; *m.p.b.*, median parietal boss or tumescence, similar in character to, but differing in position from, the lateral bosses of Giraffe or of Okapi or the median boss of Giraffe.

to lie nearly (not quite) in one plane. This is a primitive and an unusual character. It is more or less retained by the genus *Alces* (text-fig. 6, p. 286) and others of the Cervidæ, where the planes of the two axes form a very open angle; but in the Bovidæ a much less obtuse angle is formed by the plane of the basicranial axis where it meets that of the basifacial axis (text-fig. 8, p. 287).

The whole of the brain-case or postorbital region of the skull of the Bovidæ appears to be bent down as on a joint formed across the junction of the cranial and facial portions of the skull (see text-figs. 7 and 8, p. 287). This bending down or angulation of the brain-case has occurred to some extent in *Giraffa*, as shown in the section (text-fig. 5, p. 286), but much less than in the Bovidæ. Although our specimens of Okapi's skull have the basis cranii broken away, we can yet conclude confidently from the relations of the roof and sides of the cranium that there was a complete absence of any such bending or of any angle at the junction of the basicranial axis with the basifacial axis.

There is good ground for connecting the presence of the deflection of the cranial cavity, above noted, with the mechanical conditions arising from the use of horns having the position and direction of those found in Bovidæ and the Giraffe. Even in the hornless females of certain Antelopes the deflection is maintained (text-fig. 7, p. 287). The absence or small size of the deflection is almost certainly to be regarded within the group Pecora as a primitive character, and in the horizontality of the skull or tendency to coincidence of the basicranial and basifacial axis-planes the Okapi bears

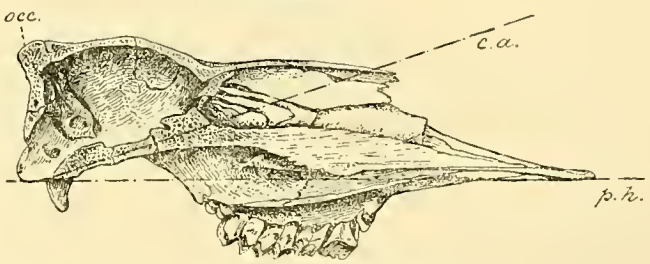
Text-fig. 5.



Vertical longitudinal section of the skull of a Giraffe, to show the air-sinuses and the relatively low angle formed by the basicranial axis (*c.a.*) and the palatine horizontal (*p.h.*).

occ., occipital crest; *p.oss.*, parietal ossicusp; *g.t.m.*, Giraffe's median tumescence, upon which the median osseous cap develops.

Text-fig. 6.



Vertical longitudinal section of the skull of a female Elk (*Alces*), to show the low angle formed by the basicranial axis (*c.a.*) and the palatine horizontal (*p.h.*).

occ., occipital crest.

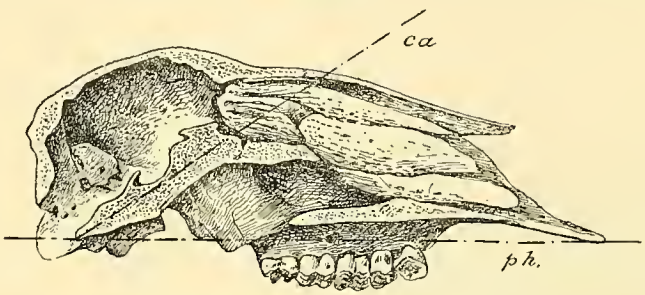
evidence of (1) being relatively primitive, (2) not having had horn-bearing forebears, (3) of being remote from the Cavicorn stock.

A further character, at once obvious on examination of the Okapi's skull, is the absence of the lacrymal fossa—present in many Antelopes and all the Cervidæ, but absent in Giraffes. This, however, is not a diagnostic character, since the lacrymal fossa is not present in all Antelopes. Equally inconclusive is the existence of the "prælacrymal vacuity" (Pl. XXXII. fig. 12, *c*), which is well marked in the Okapi's skull and in all

Giraffe skulls, except those of old individuals. The prælacrymal vacuity occurs in other Pecora besides the Giraffe, being well developed both in *Alces* and in *Antilocapra* and other Cervidæ and Bovidæ.

We have not so far found any character, beyond the general shape of the skull, which tends to associate the Okapi with Giraffidæ rather than with Bovidæ or Cervidæ. And, as a matter of fact, though an enumeration of details, such as shape of the nasals and each of the cranial bones, the absence of lacrymal fossa, and presence of prælacrymal

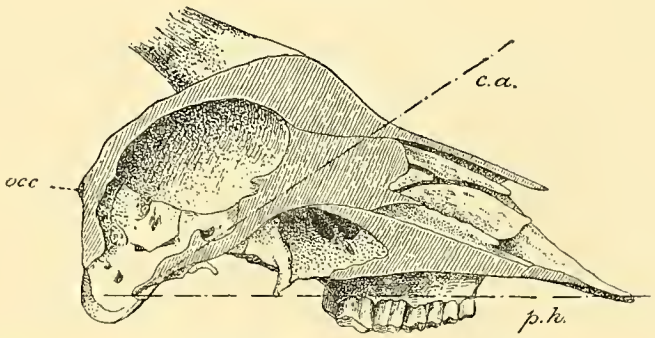
Text-fig. 7.



Vertical longitudinal section of the skull of a female Water-buck (*Kobus ellipsiprymnus*), to show the high cranio-palatine angle in a hornless Bovid.

c.a., basicranial axis; *p.h.*, palatine horizontal.

Text-fig. 8.



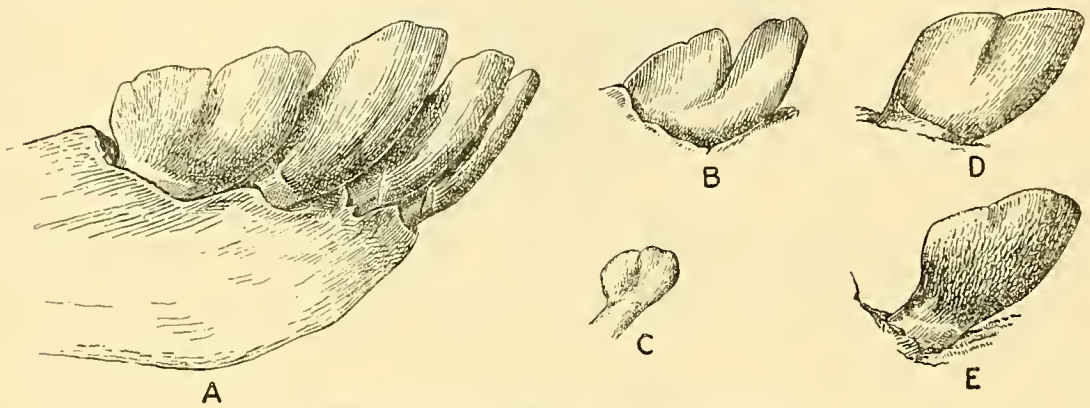
Vertical longitudinal section of the skull of the Domestic Goat (*Capra*), to show the high angle formed by the cranial axis (*c.a.*) and the palatine horizontal (*p.h.*).

occ., occipital crest.

vacuity, would result in a totality of agreements with *Giraffa* greater than with any other form, still we have not yet mentioned any one character peculiar to *Giraffa* which also is found in *Okapia*. There is, however, such a character, and this is found in the peculiar bifoliate form of the crown of the lower incisor on each side. If we compare the group of eight teeth forming the biting-apparatus of the lower jaw in *Giraffa* and *Okapia*, we observe that the group of teeth is relatively larger and more widely spread (in proportion to size) in the former than in the latter. The group of

teeth is a flatter more spatula-like structure in the Giraffe than in the Okapi. In the Okapi the group is relatively small, and the individual teeth not only actually smaller but, relatively to the size of jaw and skull, very much smaller than in *Giraffa*[1]. They do not form so flat or horizontally depressed a group: there is, on the contrary, a marked concavity within the margin of the group of teeth. This difference in the relative size and in the shape of the group of incisive teeth of the lower jaw points to some marked difference in the food of the Okapi as compared with that of the Giraffe. We do not know, as yet, on what the Okapi feeds, but it is certainly not the same vegetable growth as that which is sought by the Giraffe. Nevertheless, whilst there is a marked

Text-fig. 9.



Canine teeth of Giraffidæ, all of the natural size.

A. Right permanent canine and three incisors of Giraffe.
B. Right deciduous canine of young Giraffe.
C. Right permanent canine of *Okapia johnstoni*.
D. Right permanent canine of *Samotherium* (*Palæotragus*).
E. Right permanent canine of *Sivatherium*.

These drawings were made under my superintendence from original specimens preserved in the Natural History Departments of the British Museum.

difference in the proportions of this anterior group of teeth when compared in the two animals, the remarkable fact is discovered that the Okapi has bifoliate lower canines precisely resembling those of the Giraffe. This fact alone is sufficient to bring *Okapia*—given its general Pecorine characters—into close association with *Giraffa*. The bifoliate lower canine was not hitherto known in any other of the Pecora, or,

[1] The very much smaller relative size of the front teeth of the lower jaw of *Okapia* than of *Giraffa* is shown by a comparison of the drawings given here, viz. text-figure 12, p. 293, showing the milk-dentition of this region in *Giraffa*, with the permanent dentition of *Okapia* (Pl. XXXII. fig. 12), and the text-figure 9, showing the permanent and the deciduous canines of *Giraffa*, compared with the permanent canines of *Okapia*, of *Samotherium*, and of *Sivatherium*, drawn of natural size.

indeed, in any mammal at all, excepting *Giraffa* and its extinct allies *Samotherium* and *Sivatherium* (see text-fig. 9).

The bifoliate form of the canine of the Giraffidæ has no obvious explanation. The existence of fissures in teeth of this shape and position finds a parallel in the curiously fissured incisors of *Galeopithecus*. A closer point of contact is presented by the outer lower incisors of *Sus* and *Anchitherium*, which have a distinct secondary lobe. The canines of many Insectivora present a crown with two lobes, a feature which Dr. Forsyth Major considers as pointing to the derivation of the canine from a premolar. The great development of the second plate or "folia" in the Giraffe's canine obviously serves the place of an additional tooth in increasing the amplitude of the semicircular grip of the mouth. There is no adjacent tooth on the diastemic margin of the canine to interfere with expansion in that direction, and so the accessory growth has free play. If the increase of the mouth-grip was the original motive of the selection resulting in a bifoliate canine in Giraffidæ, it seems probable that *Okapia*, with its very small mouth-grip and small incisors and canines, is not in respect of its front teeth so primitive as *Giraffa*, where both incisors and canines are of so large a size (proportionately to the other teeth) that the whole group or arch of front teeth may be regarded as having attained a maximum only capable of increase by the addition of a lobe to the outer member of the series (the canines) on each side.

The great size of the incisors and canines is especially striking in the young Giraffe with milk-dentition and a lower jaw measuring only seven and a half inches from the angle to the symphysis (see text-fig. 12, p. 293).

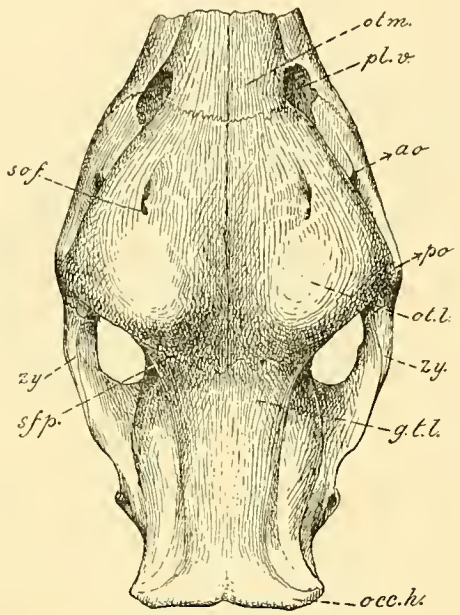
I have had drawings prepared, which are here reproduced (text-fig. 9, p. 288), showing (A) a lateral view, natural size, of the canines and incisors of an adult Giraffe, by the side of which are represented, also of the natural size, lateral views (B) of the deciduous canine of the Giraffe, (C) of the permanent canine of *Okapia*, (D) of the permanent canine of *Samotherium*, and (E) of the permanent canine of *Sivatherium*. The extremely small size of the permanent canine of *Okapia* and the large size of the deciduous canine of *Giraffa* are thus rendered very obvious.

In our lower jaw of Okapi (Pl. XXXII. fig. 12) the canine of the left side has a bifoliate crown, whilst that of the right side has the crown broken and worn away. They are obviously only milk-teeth, and on cutting into the jaw below that of the right side we discovered, as we expected to do, the fully-developed bifoliate canine of the permanent set, which is drawn in Pl. XXXI. figs. 4, 5, and in the text-fig. 9, p. 288. This agreement in a point of minute but definite detail, found in Giraffidæ and *Okapia* alone, has greater significance than any of the more general points of resemblance presented by the skulls.

An important feature in the skull of *Giraffa*, which it is difficult to define, is one which I can only speak of as "a tendency to tumescence" of the roofing-bones. This feature is common to *Okapia* and *Giraffa*. It is well known that in the adult Giraffe

the bones of the skull show a very considerable system of sinuses separating the upper and under surfaces of certain regions of what are usually flat bones (see text-fig. 5, p. 286). This "tumescence" of cranial bones occurs in various Ungulata and other mammals; but it is not developed in other Pecora in the same regions and to the same extent as it is in *Okapia* and *Giraffa*. In *Okapia* it is largely developed in the orbital region of the frontal bone (text-fig. 10), and in the adjacent parietals in *Giraffa* (text-fig. 11, p. 291). Also in both genera tumescence occurs in the expanded nasal region

Text-fig. 10.



View from above of the fronto-parietal region of the skull (larger of the two specimens) of the Okapi.

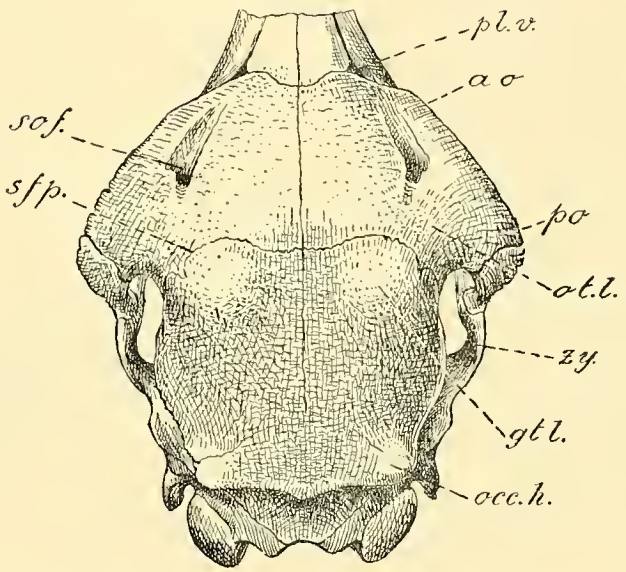
occ.h., angle of the occipital crest; *g.t.l.*, position of the lateral tumescence forming the paired parietal horns of the Giraffe, absent here; *ot.l.*, the lateral frontal tumescence of the Okapi, absent in Giraffe; *zy.*, the zygomatic arch; *po.*, posterior angle of the orbit; *ao.*, anterior angle of the orbit; *pl.v.*, prælacrymal vacuity; *otm.*, the slight median tumescence of the base of the nasals of the Okapi; *sof.*, supraorbital fossa; *sfp.*, the fronto-parietal suture.

For comparison with text-figure 11.

either in the nasals themselves or in the adjacent region of the frontals. The strong development of the supraoccipital crest in both skulls (text-figs. 2 & 3, p. 284) is not precisely of the same nature, for the thickened bone is not there excavated by sinuses. I shall revert to this matter immediately, but must here point out the remarkable form and aspect of the orbit of the Okapi, which is connected with the tumescence of the bone which forms it. The orbit is rectangular, not circular as it is in

Giraffa, and its margin is not formed by a thin upstanding rim of bony matter as it is in *Giraffa* and nearly all Pecora, but is heavy, rounded, and thick. This seems to me to be an archaic character—the sharp thin edge of the orbit being a modern and truly Pecorine development. It is, nevertheless, found that the double notch, or pair of notches, on the lacrymal border of the orbit have precisely the same position and character in (what I am constrained to regard as) the archaic orbit of *Okapia* as in the modernized orbit of *Giraffa*.

Text-fig. 11.



View from above of the fronto-parietal region of the skull of a very young Giraffe. The parietal epiphyses were already ossified, but separable, and are here removed.

occ.h., exostosis of the occipital crest, which in some adult Giraffes forms a second pair of "horns" (five-horned Giraffe); *gtl.*, the Giraffine lateral tumescence, seen here to originate in the parietal bone, which carries the conical epiphysis and forms the Giraffe's paired "horns"; *ot.l.*, the position of the Okapi's lateral tumescence of the frontal bone, absent in Giraffe; *zy.*, zygomatic arch; *po.*, posterior angle of the orbit; *ao.*, anterior angle of the orbit; *pl.v.*, prælacrymal vacuity; *sof.*, supraorbital fossa; *sfp.*, fronto-parietal suture.

IV.—The Areas of Tumescence of the Giraffine Skull and the Nature and Origin of the Horns of Pecora.

In order to make an intelligent comparison of the skull of *Okapia* and *Giraffa* in regard to the presence and absence of what are called "horns," it is necessary to discriminate between the varieties of horns presented by various groups of Pecora and to accept one theory or another as to their origin and relationships.

The word "horn" is a comprehensive term of various and uncertain meaning. It

applies equally to the substance "keratin," of which many horns largely consist, and to the antler of the Stag, which has no horn about it. The "horn" of the Rhinoceros consists of a solid fibrous growth of keratin, resting on a slightly raised bony boss. There is no "horn" of this structure known among the Pecora. There are living Pecora and there are allied living and extinct forms devoid of all trace of those growths on the head which are called horns, whether of this or of that variety. Horns appear, in proportion to their size and dominance, to be structures easily acquired and easily lost, for they are often absent in the female whilst present in the male. They are absent in both sexes in some domesticated races and present in others of the same species; and, further, whilst commonly only a single pair are developed in Pecora, yet a second pair may occur in a genus (*Tetraceros*) otherwise differing little from genera with a single pair, and in domesticated races (Sheep) we have well-marked strains without horns, with one pair, with two pairs, and even three pairs, and with large and striking differences of shape and size.

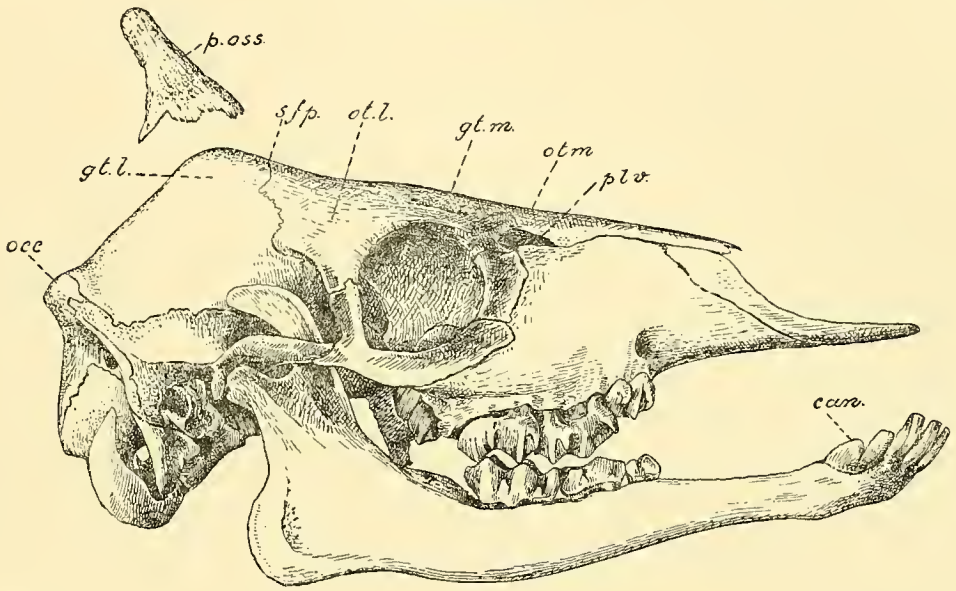
The horns of the Pecora are essentially bony outgrowths, or "ossicusps," developing on and from the roofing-bones of the skull. I definitely adopt this theory of their nature and origin, and reject that which would regard them as originating ancestrally either as horny plates or knobs of the epiderm, or as detached subepidermal bony plates like the carapace-elements of *Glyptodon* and *Armadillo*. The fact that in Bovidæ the bony horn-core or ossicusp makes its appearance as a detached plate of tissue which ossifies from an independent centre, and only fuses with the subjacent bone during ossification, does not necessitate the conclusion that this was the ancestral mode of origin of the horn.

The definite growth and selection of a pair or more "ossicusps," or exostoses, so as to reach a size deserving the name of "horns," was probably preceded by a condition of the skull in which "tumescence," such as we see in *Okapia* and *Giraffa*, was a general tendency. Rounded bosses were formed here or there, both paired and median. They gave definite point to a blow when the head was used as a battering-ram, and also by their sinus-structure made fracture a matter of small consequence. Variation and selection would emphasize one or other pair of such "bosses," or this or that median boss, differently in different lines of descent. It is not necessary to suppose that the paired horns of all Pecora are the lineal descendants of one and the same pair of "bosses" in ancestral forms. It is obvious enough that one of the pairs of horns of *Tetraceros* has an origin independent of that of the other pair, and so too with the smaller and larger pairs of horns of *Sivatherium* and the median and posterior pair of *Bramatherium*. The tendency in primitive Ungulates to develop numerous bosses on the skull, which are incipient horns, is seen in the extinct group represented by the genus *Dinoceras*, with its anterior, median, and posterior pairs of horn-bosses. The paired horns of *Giraffa* are shown by the young specimen drawn in text-fig. 12 to be distinctly related to a pair of bosses on the *parietal* bones and not to correspond

to the supraorbital *frontal* horns of Cervidæ and Bovidæ. On the other hand, the paired supraorbital frontal tumescence of *Okapia* (text-fig. 2, p. 284), whilst not identical with the paired tumescence of the *parietal* in *Giraffa*, does, it appears to me, correspond in position and probably genetically with the supraorbital "ossicusp" developed on the *frontal* bone of *Samotherium* and of the Bovidæ and Cervidæ.

From this statement, it will be evident that I regard the Giraffidæ as presenting a more generalized ancestral condition of the horn-bosses than is found in any other

Text-fig. 12.



Lateral view of the skull and lower jaw of a very young Giraffe, measuring 30·8 centimetres from the occiput to the anterior border of the præmaxilla. This is the same specimen as that represented in fig. 11, and is preserved in the British Museum. The drawing is five-twelfths of the natural size.

occ., occipital crest; *gt.l.*, Giraffine conical tumescence of the parietal bone, above which is developed the epiphysis (*p.oss.*); *sfp.*, the fronto-parietal suture; *ot.l.*, position of the lateral tumescence of the Okapi, absent here; *gt.m.*, position of the median frontal tumescence of the Giraffe, which in this young specimen is still entirely undeveloped; *otm.*, position of the median tumescence of the Okapi's skull (basinasal); *plv.*, prælacrymal vacuity; *can.*, bifoliate canine (deciduous dentition).

group of the Pecora. We have, indeed, in the Giraffidæ, taking into consideration its various extinct members, an unspecialized condition of the tendency to horn-formation. We know in them of either well-grown ossicusps or incipient osseous horn-bosses of six locally different origins, viz.: (1) paired frontal supraorbital growths (*Okapia*, *Samotherium*, small pair of *Sivatherium*); (2) paired parietal growths (*Giraffa*, *Sivatherium*, *Bramatherium*); (3) paired occipital growths (large hinder pair of *Bramatherium*, small pair of five-horned Giraffe); (4) median nasal growth (at the base

of the nasals in *Okapia*); (5) median frontal growth (in *Giraffa*); and (6) median parietal growth (in *Helladotherium*, text-fig. 4, p. 285, *m.p.b.*). It is not in every case that these "bosses" or "tumescences" of the skull-wall have gone on to form well-marked "ossicusps," still less have they always given rise to an ossicusp of such size and importance that it has acquired an independently ossifying cap or epiphysis. The occipital exostoses of the five-horned Giraffe are well-marked knobs, but do not appear to have independent ossification. On the other hand, the paired parietal and median frontal horns of the Giraffe are prominent conical elevations of the outer plates of the parietal and frontal bones respectively, separated by large air-sinuses from the deeper plate and "capped" (but not by any means solely constituted) by superficial cones of bony matter, which ossify independently of the tumescence or boss of the cranial bone on which they rest (see text-fig. 12, p. 293).

An interpretation of the separate ossification of these pieces and of the early independence or separation of the ossicusps in the Bovidæ appears to find favour with many zoologists, which I regard as erroneous. It is supposed that these bony pieces have not originated from the skull, but are ancestrally independent dermal bony plates which become fused to the skull. I think that this is an erroneous interpretation of the facts. On the contrary, I think that just as the marked and outstanding processes of other bones in the mammalian body (such as trochanters, vertebral apophyses, &c.) acquire independent ossification, and appearing as "epiphyses" ultimately fuse with the bone of which they are in reality and origin only *outgrowths* (apophyses), so do the ossicusps of the Pecorine horns acquire in many cases an independent formation, which is related to their great size and importance, and is not a retention or exhibition of ancestral independence. It is obvious that our whole view of the relations of the "horns" of the Pecora to one another depends on the answer to this question—"Can a cusp-like outgrowth of a cranial bone, developed in continuity with that bone, be the genetic equivalent of a cusp-like structure which has in late embryological stages a detached appearance and an independent ossification, and becomes only after such a period of separateness united to the subjacent cranial bone?" An investigation of the embryological facts in the Bovidæ at a stage earlier than that described by Brandt[1],

[1] See A. Brandt, "Ueber Hörner und Geweihe," Festschrift Leuckarts, 1892. Recently Dr. J. Ulrich Dürst has published a valuable essay, entitled, "Versuch einer Entwickelungsgeschichte der Hörner der Cavicornia," in the Festschrift zur Feier des 70. Geburtstages von Prof. Dr. Ad. Kræmar (Frauenfeld, 1902), for the opportunity of seeing which I am indebted to Dr. Forsyth Major. Among the more important points established by Dürst is the fact that the separated rudiment of the horn-core which appears in young Bovidæ is not cartilage (as sometimes asserted), but, as one would have supposed, osteogenetic tissue.

It seems that we still do not possess a really thorough histological and embryological study of the ossicusp or bone of the horn and antler of Pecora.

I venture (as modifying somewhat what I have said in the body of this memoir) to put forward the hypothesis that whilst the primitive element of the ossicusp is an outgrowth of the outer table of a cranial bone, a secondary accessory bony element has been developed upon and in connection with this which has a

and a more minute histological study of the cellular origin of the tissues involved, would probably give a decisive result in regard to this question. We have to note that in the case of these cranial bony outgrowths we are dealing with tissues of very special activity and variability. The annual detachment and breaking away of what is admittedly a true outgrowth of the frontal bone in the Cervidæ and its regrowth, the suppression of Pecorine horns altogether in races and individuals, as well as their duplication, indicate that these bony growths cannot be in any case regarded as *mere* processes of the bone of which they form part in the adult. That such was their ancestral origin seems most probable; but quasi-independence and peculiar nutritional relations have been subsequently acquired by them.

The theory that the Giraffine and Bovine horn-cores—as distinct from the Cervine antler—have originated ancestrally from independent dermal bones, distinct from the cranial roofing-bones, involves one of two suppositions, viz., either that the dermal

---

characteristic histological structure, and is referable to the same class of bony growths as those produced pathologically in cases of rheumatic arthritis. This secondary element of the bony core of the Pecorine horn is seen in a comparatively unmodified condition as the hollow cone-like caps or epiphyses of the horn-cores of *Giraffa*. I suggest as probable that the caducous portion of the Cervine antler is genetically identical with this epiphysial cap, whilst the base or "Rosenstock" of the Cervine antler is identical with the more or less protuberant boss or tumescence which is a direct outgrowth of the outer tabula of a cranial bone in Giraffidæ. In vertical sections now before me of the bony horns of full-grown Giraffes, it is evident that this basal (and more primitive) element of the ossicusp is of considerable volume, and actually rises up some four or five inches, so as to form the base and axis of the parietal horns, the epiphysial cap having the form of a *hollow cone* which rests on and is fused with this deeper cone-like upgrowth. I find myself in agreement with Dr. Dürst, who recognizes the existence of this truly frontal upgrowth in Cavicornia as "Hornstiel," and identifies it "in gewisser Hinsicht" with the "Rosenstock" of Cervidæ.

The "Hornstiel," or horn-pedicle, or horn-boss, though small, is present in varying degree, according to Dr. Dürst, in all Cavicornia. On the other hand, the "Hornzapf," or horn-cone, of the Cavicornia (as distinguished from the horn-boss) originates as a mass of osteogenetic tissue, separate from that which forms the frontal bone; it constitutes by far the greater bulk of the bony structure of the horn. It seems to me probable that the Cavicorn's bony horn-cone is identical with the hollow conical bony epiphysis or cap of the Giraffe's horn, and, consequently, with the deciduous element of the Cervine antler. In Cavicornia the primitive bony element of the horn, viz. the horn-boss, or Hornstiel, has been further reduced than it is in the Giraffe, and its place is actually taken by the secondary accessory structure—the horn-cone or epiphysial cap. A secondary growth, originally developed as an accessory to a primitive organ, has here (as happens in other instances) acquired overwhelming vigour, and been substituted for the primitive organ, which consequently dwindles and nearly disappears. The Giraffes, with their well-developed cranial horn-bosses and relatively small epiphysial horn-caps (Hornzapffen) are intermediate between the Cavicorns and a primitive group which had no epiphysial horn-caps, but only horn-bosses (Hornstiele). Our immature *Okapia* is actually in the latter condition, and it seems (so far as adult specimens can allow one to judge) that the horn-cores of the long-extinct Dinocerata also were true horn-bosses of the cranial bones and not epiphysial—that is to say, not "Hornzapffen," or horn-caps.—E. R. L., April 30th, 1902. The actual mode of growth of the frontal "ossicusps" three inches in length, revealed in the adult Okapi recently received in Brussels, has yet to be ascertained.—May 23rd, 1902.

bones in question are survivors of a general dermal cuirass, such as we see in *Armadillo*, *Glyptodon*, and *Mylodon*, or that they are new formations. The absence in other Ungulata of dermal bones of either class renders it more probable that the "separateness" of the horn-cores of *Giraffa*, and in a less degree of Bovidæ, is an acquired feature comparable to (if not identical in detail with) the "separateness" of trochanteric and other epiphyses of bones in other parts of the skeleton. It is worth noting in this connection that in skulls of old male Giraffes the periosteum at various points—*e. g.*, an additional median site and supraorbital sites—becomes active and deposits rough growths of bones (exostoses), resembling those seen in old rheumatic limb-bones of Man.

The horns of Pecora, in reference to their complete structure and history, may be grouped in four categories:—

1. The Vellericorns of the living Giraffidæ, with soft hairy integument covering the ossicusp: the ossicusp either a cone-like upgrowth of the outer table of a cranial bone with an accessory separately-ossifying "cap" or epiphysis or else a simple exostosis (occipital horns of 5-horned Giraffe).
2. The Cavicorns of Bovidæ, with a horny theca: the ossicusp before ossification appearing as a knob of soft tissue separated from the subjacent cranial roof, but subsequently fused to it.
3. The Caducithecal Cavicorns of *Antilocapra*, with a horny theca which is shed and replaced annually.
4. The Antlers of Cervidæ, direct outgrowths of the outer table of the frontal bones, clothed in an early stage with soft hairy integument, as in the vellericorns of Giraffidæ, but losing this integument and exposing the distal portion of the bony ossicusp, which dies, is shed, and regrown annually, whilst the basal portion (Rosenstock) remains in perpetuity as part of the frontal bone.

The cavicorns of the Bovidæ can be readily derived hypothetically from frontal vellericorns in such a position as the ossicusps of the Giraffid *Samotherium* (= *Palæotragus*). The development of a *permanent* horny theca on the integument covering the ossicusp necessitates, if the horn so formed is to increase in size, that it shall grow only from the base: that is to say, it cannot develop branches which shall grow in proportion with the rest of the horn. Hence the permanent cavicorn is unbranched.

The vellericorn covered by soft growing integument meets of course with no obstacle in assuming a branching form in the course of growth, and perhaps the palmate horns of *Sivatherium* were vellericorns. The form of the posterior horn-cores of *Bramatherium* is, however, so much like that of a bovine horn-core that it seems probable that these extinct Giraffidæ had developed a horny theca upon the integument of their horns. In that case the palmate horns of *Sivatherium* not improbably had also a theca which they must have shed from time to time during growth.

The caducithecal cavicorn of *Antilocapra* is, it seems, the sole modern example of the combination of horny theca with branched or prong-bearing form. If we assume that, starting from conditions more or less closely similar to those exhibited by the vellericorns of *Giraffa*, there was, so to speak, a demand for a large branched prong-bearing horn, there would be two alternative modes of meeting the demand. The integument might be left unprotected and soft on the growing antler, in which case it would tend to be seriously damaged and torn by blows, or it might be protected by a theca, periodically shed and renewed. A periodicity in the nutrition of the horn-structures would be established in the latter case. In the former case the exposure of the bony mesoblastic tissues by abrasion of the integument would tend to necrosis of the bone and serious danger to the animal. It would thus be an advantage that the exposed dead bone of the antler should be shed and a new formation take place at intervals. The establishment of a relation between this and the nutritional activity of the recurring annual process of sexual ripening is not an improbable thing. The periodicity of the horn-shedding of the caducithecal forms and that of the antler-shedding forms may well have had a common origin.

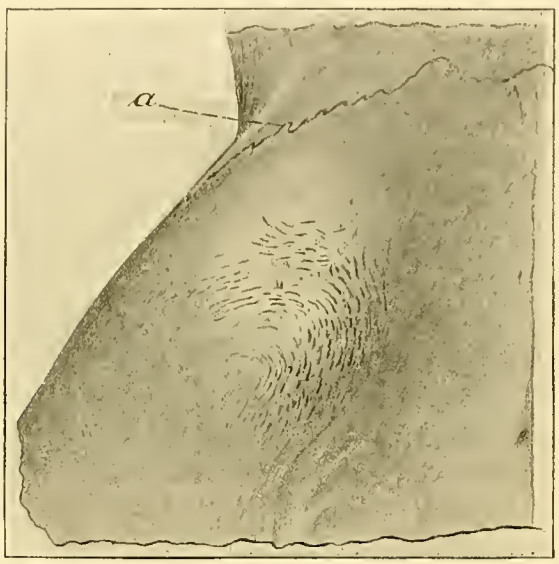
The antlers of Cervidæ seem thus to be an outcome of the simple short vellericorns still retained by the Giraffe, and the three structures—viz. unbranched Cavicorns, Caducithecal Prong-horns, and naked regenerative Antlers—are three distinct lines of development of Pecorine horns of increased strength, amplitude, and resistance, from conditions present in ancestral Giraffidæ. These varieties of horn-structure were probably more or less completely differentiated within that group, or in a more generalized set of forms antecedent to it.

Whilst thus referring the various forms and structures of Pecorine horns to primitive conditions retained by Giraffidæ, I do not overlook the fact that in regard to other important structures the Giraffidæ do not exhibit archaic features. The great length of the diastema in the dental series and the complete absence of upper canines are points in which Giraffidæ are not primitive, as also is the total suppression of the pettitoes. In possessing often well-developed, even extremely large, canines the Cervidæ are more primitive than the Giraffidæ; and both Cervidæ and most Bovidæ, in the frequent presence of well-developed extra digits, retain an ancestral feature lost by Giraffidæ. There is, however, ample ground for supposing that in the differentiation of lines of descent from the primitive Pecora one group may have retained one set of characters in a primitive condition and another group another set.

I propose now briefly to revert to the Okapi's skull and its "bosses" or "tumescences." It is, of course, possible, as our larger specimen is only two-thirds grown, that a separate "ossicusp" was destined to develop over each of the supra-orbital bosses (*otl.* in text-fig. 2, p. 284). There does not appear to have been any rudiment of such a structure in the dried skin of the head as removed by the

natives and received in this country[1]. But there is evidence that the integument was very closely applied to the bone of the supraorbital bosses and that there was a specially vascular condition of the periosteum in the centre of the boss. A figure (text-fig. 13) of this appearance is here given. The hair on the integument is arranged so as to converge on the centre of the boss, and there is a distinct upstanding of the hairs around it and a bare spot at the actual centre (text-fig. 14, p. 299, *a* and *c*). The arrangement

Text-fig. 13.



Drawing (natural size) of a portion of the skull of the Okapi (larger specimen), to show the surface of the right frontal boss. The surface of the bone shows numerous grooves occupied by blood-vessels, indicating that the periosteum was here in close vascular continuity with the subcutaneous connective tissue.

[The peculiar vascular condition of the surface of the bone at the supraorbital tumescence now receives its explanation in the later growth here of the bony tissue to form the large conical ossicusp.—May 27th, 1902.]

of the hair over the two orbital bosses (*a* and *c*) and above the nasal tumescence (*d*), as shown diagrammatically in text-figure 14, p. 299, is very remarkable.

It is improbable that at this age and size our Okapi, if a male, had yet to develop

[1] The existence of such a rudiment was at first supposed by me to exist, and a notice by me in an illustrated weekly paper is quoted by Dr. Dürst (*loc. cit.*) to that effect. I found, however, on cutting open the skin of the head after it had been received from the taxidermist that there were no thickenings of the integument over the frontal bosses, but that the taxidermist had taken the liberty of inserting a small plug of cotton-wool over each frontal boss, so as to give a strongly marked prominence to the integument in this position.—E. R. L., April 30th, 1902. It now appears (May 23rd) that my original supposition was probably correct, since the Brussels skull of an adult Okapi shows ossicusps three inches in length, though their mode of growth is not yet ascertained.

Text-fig. 14.

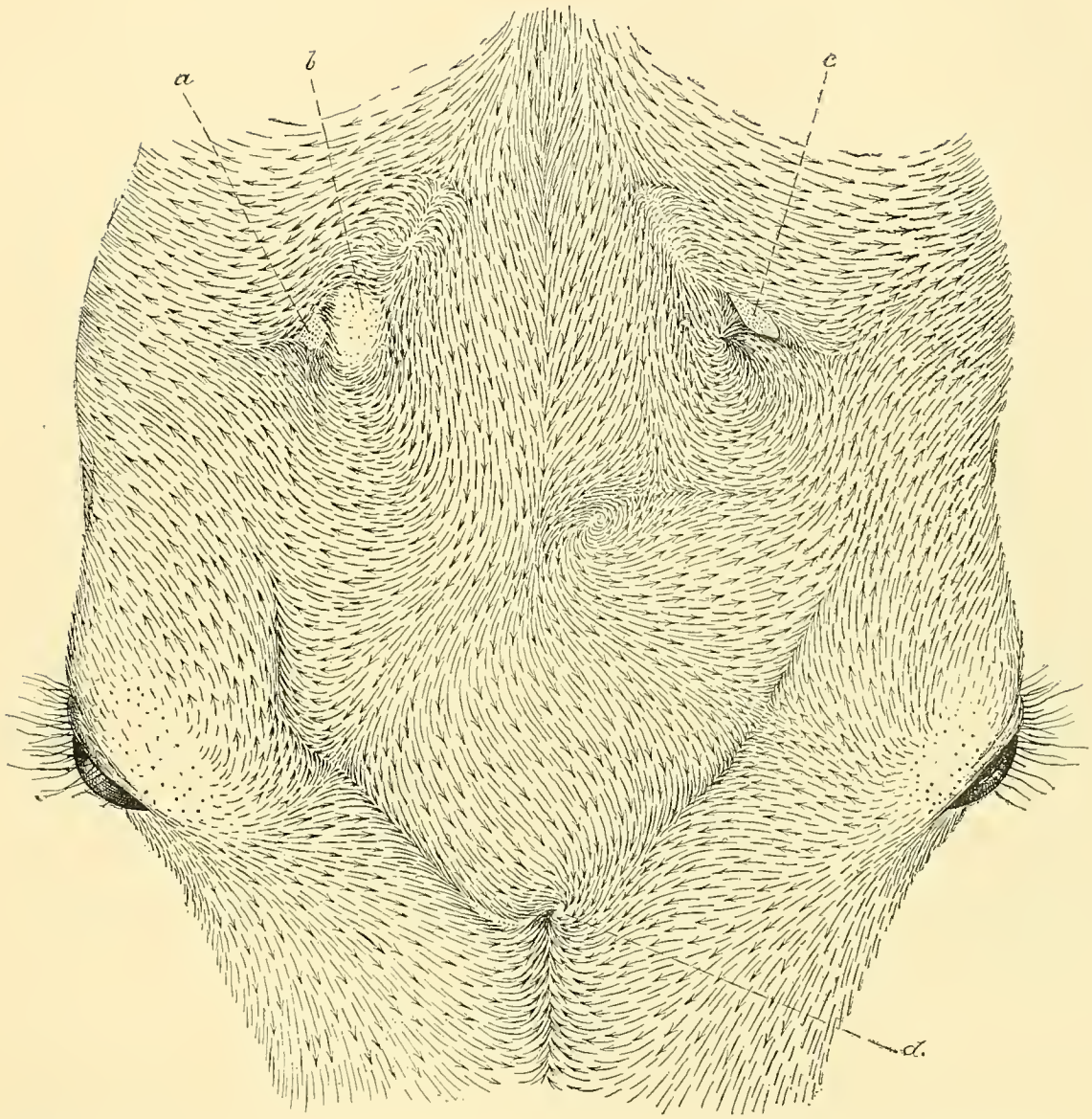


Diagram to show the arrangement of the hair upon the frontal and basinasal regions of the Okapi's head. The *free* ends of the hairs are represented by the points of the arrows. *a* and *c* are natural bald spots overlying the apices of the boss or tumescence of the right and left frontal bones. *b* is a bare spot, probably due to abrasion. The tuft of hair below *c* is well-marked, but is absent on the opposite side of the head. The whorl marked *d* corresponds in position with the slightly tumescent base of the nasal bones. The unlettered whorl, near the middle of the figure, possibly owes its position to the left of the mid-line to unequal stretching of the skin by the taxidermist. The study of the hair-whorls on the head of various Mammalia may yield important data for systematists, but has not yet been methodically carried out.

any separate horn-cap or epiphysis, but it may well be that the supraorbital boss becomes more accentuated in the adult or old male.

On the other hand, supposing our older specimen to be a female, it is possible that the male has much more pronounced horns. It is impossible to decide whether our large specimen is male or female, and we must await the arrival of further specimens of the Okapi for information on the subject.

The bases of the nasal bones are slightly thickened or swollen in the Okapi (as shown in text-fig. 2, p. 284, *otm.*, and in Plates XXXI. & XXXII.). This swelling is thus in front of the region carrying the median boss of the Giraffe's skull, just as the paired lateral swellings are anterior to those of the Giraffe. In *Helladotherium* there are no lateral "bosses," but a median boss is present which is further back even than in the Giraffe, and is distinctly parietal in position (text-fig. 4, p. 285, *m.p.b.*). A spiral arrangement of the hair of the Okapi's face corresponds in position to this slight thickening of the nasal bones (see text-fig. 14, p. 299, *d*).

There are those who would interpret the apparently hornless condition of *Helladotherium* and *Okapia* as due to a degeneration and loss of horns, present and well developed in ancestors of these genera. On the other hand, it is possible to regard these two forms (if actually proved to be hornless) as being in a primitive condition, having developed the bosses or tumescences which are the first step in the history of horns, but never having got any further. It does not seem to me possible to decide between these two theoretical views; but I am inclined, on account of the absence of a deflection of the basicranial axis from the horizontal of the basifacial axis or palatine, to infer that neither *Okapia* or its ancestors ever possessed *large* frontal horns—not even horns so large as the parietal horns of *Giraffa*. The possession and use of such horns (as distinguished from laterally-spread antlers) seems to involve the mechanical necessity of a deflected cranial floor. Even *Giraffa* exhibits such a deflection in small degree (see text-fig. 5, p. 286).

V.—Characters presented by the Skin of the Okapi.

The skin of the Okapi, when received in London, was in very good condition. The paired ungual phalanges were still attached to the skin, but the horny hoofs had been lost. The skin was softened and mounted for the Natural History Museum by Mr. Rowland Ward. It must be remembered that no white man has as yet seen, or at any rate given any account of, a living Okapi, nor even of the body of one freshly killed. Nor have we received the skeleton of any part except the skull and hoofs. Accordingly the proportions assigned to the various parts of the animal and the carriage of its head and neck are, to a certain extent, conjectural and determined by the proportions of the skin only, as thus received. The animal, as mounted, is shown in the two drawings given in Plate XXX. with the natural colours.

The chief point of doubt in the result obtained by Mr. Rowland Ward is as to the carriage of the head and neck. He has, in agreement with me, made the neck continue the line of the back as it does in the Giraffe and some of the Antelopes. It has been suggested that the neck should rise nearly vertically from the shoulders and form more of an arch, as it does in some Ungulates; but we have no information as yet to guide us in the matter. It is quite certain that all the old drawings and mountings of the Giraffe, which represented that animal's neck as rising vertically with a graceful curve from the shoulders, are erroneous. The Giraffe's neck is habitually carried in a line which is a continuation of the rising line of the back from haunches to withers. The neck inclines forward, with the head projecting far in front of the fore legs, whether the Giraffe is at rest or in movement. It is only when the Giraffe is reaching with the mouth at some object higher than the head that the neck assumes a vertical position.

The following are the measurements of the skin of the Okapi as mounted:—

		feet.	inches.
From occiput to root of tail	1860 mm. =	6	2
From occiput to muzzle	520 mm. =	1	9
From occiput to withers (length of neck) . . .	870 mm. =	2	11
From withers to root of tail	990 mm. =	3	3
Height at withers	1530 mm. =	5	1
Height at rump (through head of femur) . . .	1370 mm. =	4	7
Length of auricle of ear from constricted base to tip.	232 mm. =	0	9
Breadth of auricle of ear	142 mm. =	0	$5\frac{1}{2}$

The most noticeable features in these proportions are, first, the much greater height of the fore-quarters than the hind-quarters, the great length of the neck, the great length of the ears. In the first two points mentioned the Okapi resembles the Giraffe, which, however, has the same features in an exaggerated degree. In the proportionate length of its ears the Okapi greatly exceeds the Giraffe.

The hairy coat of the Okapi resembles that of the Giraffe and Zebra in length and quality.

The colour of the animal is shown in the figures accompanying this memoir. The hair on the body and neck and the top of the head from the occiput to the nostrils and the ears is of a rich reddish brown, whilst that on the side of the face is a creamy white.

The rump and hind legs, as far as the tarsal joint, are striped transversely with alternate bands of dark chocolate (almost black) and brownish-white hair. A curious feature is the reddish-brown colouring of the narrower parts of the white stripes, which gives the impression that the colour has "run" from the darker stripes. The

pattern of the stripes on both the hind and fore limbs is difficult to describe, and can best be judged of by the figure given in Plate XXX. and by the woodcut of the bandoliers (text-fig. 1, p. 281) cut from another individual. There appears to be a small range of individual variability in the exact proportions of the dark and light stripes.

The true foot—that is to say, the part of the leg extending from the calcaneum to the hoof inclusive—is white with a dark girdle encircling the first phalanx and leaving a white circle between itself and the hoof, which was seen by one of Sir H. Johnston's officials before it was lost, and reported to be blue-black in colour.

The upper region of the fore limb is of the same colour as the trunk; black and white striping is not developed upon it until we come to the region of the forearm or radio-ulnar region. This is encircled by a few narrow and two incomplete broad bands of black hair separated by bands of white. The carpo-metacarpal region is peculiarly marked: an oblong disc of white hairs is found on the carpus encircled by black. The black hairs extend as a thick band round the back of the carpus, the white disc having a nearly median frontal position. From the black ring extends downwards over the front of the metacarpal region a thick black band lying a little to the outer side of the mid-line. This black band joins a ring of black hair which encircles the phalangeal region as in the hind foot, the rest of the hair being creamy white. The appearance of this upper upright ring, bar, and lower transverse ring joined to form one piece is very remarkable and calls to mind the shape of a leg-iron or shackle such as is fastened to the legs of convicts. It probably has some significance in producing illusion when seen by the enemies of the Okapi; but it is difficult to imagine its exact effect. I have not been able to find a closely similar marking in any other animal except in certain goats—especially the Wild Goat of Asia Minor (*Capra ægagrus*). The corresponding region is very similarly marked in specimens of that animal preserved in the Natural History Museum. The one-sided position of the vertical bar is very striking and tends to give an unreal and distorted appearance to the leg.

VI.—Characters of the Genus *Okapia* and of the Species *O. johnstoni*.

At the Meeting of this Society on June 18th, 1901, I established the genus *Okapia* for the reception of the Okapi. A brief account of the skin and skulls was published by me in the Proc. Zool. Soc. 1901, vol. ii. p. 280. I now amend the characterization of the genus in some important respects[1].

The "Pecora" are ruminant Artiodactyle Ungulates with a cotyledonary placenta and are divisible into the Cervidæ, Giraffidæ, Antilocapridæ, and Bovidæ.

[1] May 27th, 1902.—So as to take cognizance of the fact as to the existence of bony frontal horns in the adult, revealed by the specimen received in Brussels a month ago. See Appendix, p. 304.

The characters of the Giraffidæ are as follows:—"Pecora with no canines in the upper jaw, with bifoliate crown to the canines of the lower jaw; with complete suppression of the second and fifth digits of both fore and hind feet; without lacrymal fossa; with horn-bosses or ossicusps of variable position (frontal, parietal, occipital, and nasal) not necessarily restricted to a single pair, often one or all rudimentary. In the living genus *Giraffa* the horns are vellericorns, but probably in some extinct genera they developed a horny theca (cavicorns), and in others may have been exposed as naked antlers."

Using the foregoing definitions of the groups Pecora and Giraffidæ, the genus *Okapia* may be characterized as follows:—

"Giraffidæ with a pair of supraorbital frontal horn-bosses, bearing in the adult well-marked conical bony horns or ossicusps. The horns covered (except at the tip) by hairy integument, not by a keratose theca. A median tumescence of the nasal bones, but no median horn (ossicusp). Plane of the basicranial axis and the basifacial axis approximately parallel. Arch formed by the front teeth of lower jaw small and narrow; individual incisors and canines relatively very small. Outer ears large."

N.B.—*Okapia* is thus contrasted with *Giraffa*, in which the paired horn-bosses are parietal instead of frontal, and in which also a median frontal tumescence and bony cap develop; and with *Helladotherium*, in which there are no paired horn-bosses. It is further contrasted with *Giraffa* (and all other Giraffidæ) in respect of the small size of its mandibular arch of incisors and canines. This is the only point in which it differs from *Samotherium* (*Palæotragus*), unless further study of the nature and development of the frontal horns should establish a difference between it and this genus. It differs from *Giraffa* in the great size of its external ears.

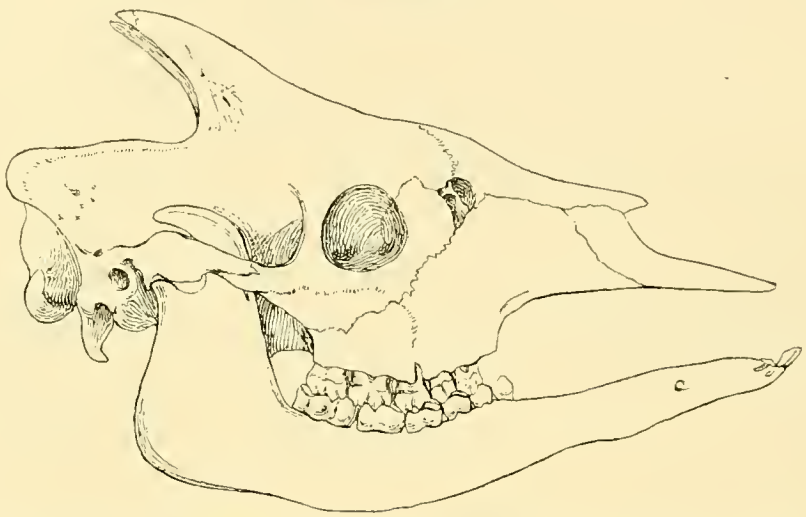
The genus *Okapia* contains a single species, *O. johnstoni*—the *Equus johnstoni* of Sclater (P. Z. S. 1901, vol. i. p. 50). The species was originally based upon pieces of the striped skin from the hind limbs, and may be defined as follows:—

O. johnstoni (Sclater). *Okapia* with the *hind limbs* (rump, femoral and tibial region) striped with alternate bands of blackish brown and white; tarso-metatarsal region white: *fore limbs* marked with a shackle-pattern—black on a white ground—on the carpus and metatarsus, radial region transversely striped. Body, neck, rump, and upper part of fore limbs a uniform rich reddish brown; side of the face white, top of the head reddish brown. Tail brown, tapering, with subterminal tuft of long hair. Mane absent.

VII.—APPENDIX. (*May 27th*, 1902.)

Since this memoir was ready for press (actually in second revise) the Museum of the Independent State of the Congo received (at the beginning of May) in Brussels, through the agents of the State stationed on the Aruwimi, near Fort Mbeni, the place where Sir Harry Johnston's specimen was obtained, a skin of an adult female Okapi, and a nearly complete skeleton of an adult male. The actual locality from which the specimens come is stated to be Mawambi. Dr. Forsyth Major has been entrusted by the authorities of the Congo Independent State with the study and description of these

Text-fig. 15.



Skull of adult male Okapi. Outline drawn from the skull of the adult male belonging to the Museum of the Independent State of the Congo.

The drawing represented the left side, but has been reversed for comparison with the figures in the present memoir. Note the large ossicusps; the divided prælacrymal fossa; the molars, of which the first upper premolar is lost; and the defective canines and incisors.

important specimens, and has been to Brussels to examine the material. The skull and various bones of the adult male have been sent to him in London since his return, for further examination. I owe an opportunity of examining the skull to the courtesy of Dr. Forsyth Major, who is carrying on his work on the subject here, in the Natural History Museum.

A full account of the new specimens will be published by Dr. Forsyth Major in the Memoirs of the Museum of the Congo State. It is not of course to be expected that I should here anticipate the interesting results which will be given in Dr. Forsyth Major's full account of the new specimens, but I am able to state a few of the more striking

facts, and to include in the present memoir an outline sketch, prepared under his direction (text-fig. 15, p. 304), of the skull of the adult male.

The specimens received in Brussels in May 1902 are the skin of an adult female and the skull and most of the bones of an adult male. The male skull bears (as shown in text-fig. 15) bony horn-cores of a conical shape, about three inches in length. They are much deflected so as to point backwards. In the skin of the female (Dr. Forsyth Major states) there are (although the skull is wanting) bony horn-cores of about two and a half inches in length. The dentition of the male skull and of the lower jaw belonging to it are well preserved, and leave no doubt as to the adult character of the specimen. It is remarkable that, whilst differing greatly in age from our larger specimen, and having developed the large and powerful bony ossicusps which are only represented by the frontal tumescences of our skull, yet the new adult male skull is very little larger than our larger specimen. The measurements of the two are as follows:—

	Sir Harry Johnston's larger specimen.	Male adult skull, Brussels.
From occipital crest to front margin of nasals . . .	375 mm.	377 mm.
Maximum width (at zygomatic arch)	182 mm.	178·5 mm.

The margin of the orbit is sharper in the Brussels skull than in ours. There is no indication of an "ossicusp" in connection with the swollen base of the nasals. The skull is in very fine and perfect condition, and will afford data for complete comparison of the base of the skull and the adult dentition with that of the Giraffe and of *Samotherium*. The periotic capsule and tympanic bulla are of much larger size relatively than in *Giraffa*. This agrees with the relatively large size of the external ear or auricle in *Okapia*.

The important and striking feature in the Brussels skull is the presence of supra-frontal ossicusps. The doubts expressed in my memoir in the preceding pages are thus resolved. Though I had definitely recognized the possibility of the development of such ossicusps in older specimens than ours, yet it must be admitted that I was inclined rather to favour the supposition that outgrowths of so large and well-developed a character as those which are now shown to exist would not be found in the adult Okapi. Their presence tends to bring *Okapia* into very close agreement with *Samotherium*. It is remarkable, in view of what is known as to the development of the ossicusps on the parietals of *Giraffa*, that *Okapia* should attain to practically adult size without having its ossicusps more strongly developed than they are in Sir Harry Johnston's larger specimen. I can hardly doubt now that some osteogenetic, if not actually osseous, cone was present between the skin and the supraorbital tumescence of the frontal in that specimen and was lost in cleaning the skin.

We do not yet know the facts as to the mode of development of the horns of the

Okapi. The fine bony cones, three inches long, which have made their appearance in the Brussels skull (see text-fig. 15, p. 304) show no suture at their base, or any indication of origin as distinct cap-like structures. For all that one can see, they may be direct outgrowths of the frontal bone itself. Curiously enough, the point and posterior margin of the bony cusp is polished as though it had protruded through the skin like a cervine antler. The point is separated by a suture from the rest of the ossicusp, forming a small terminal cap of bone a third of an inch in depth. This curious structure, as well as a possible second suture a little lower down the ossicusp, was pointed out to me by Dr. Forsyth Major. These appearances will be figured and discussed in that gentleman's memoir on the Brussels specimens. It is clear that we must wait for specimens of intermediate growth in order to form any conclusions as to the *mode of growth* of the Okapi's ossicusps. It seems not improbable that when we have those facts, important light will be thrown on the relationships *inter se* of the various cranial ossicusps of Giraffidæ, Cervicornia, and Cavicornia.

It is perhaps worth while calling special attention to the fact that Sir Harry Johnston's larger skull of *Okapia* is very nearly as long as the adult male skull recently acquired by the Congo State Museum; there is only two millimetres difference in the length from the occiput to the end of the nasal bones. Sir Harry's specimen is actually broader by three and a half millimetres than the Brussels skull. And yet Sir Harry's specimen has no ossicusps and shows the fronto-parietal suture clearly, whilst the Brussels specimen has bony ossicusps three inches long and absolutely continuous with the frontal bone, whilst the fronto-parietal suture is obliterated. Perhaps the difference of form and the late appearance of the ossicusps in our larger specimen as compared with the Brussels skull are due to the fact that our specimen is a female, whilst (according to direct testimony of the senders) the Brussels skull is that of a male. We have yet to hear further details as to the bony horn-cores reported by Dr. Forsyth Major as embedded in the skin of the head of the second Brussels specimen, which is known to be that of a female, and of which neither skeleton nor skull accompany the skin. These detached horn-cores of the female are stated by Dr. Forsyth Major to be two and a half inches long.

A further point to which I may draw attention is that there is considerable want of symmetry in the Brussels skull, in so far as the size of the bony horn-cores is concerned. One is distinctly larger than the other. Now it is a curious fact that the skin of the head of our Okapi shows, as I have pointed out (text-fig. 14, p. 299), a marked asymmetry in the hair-whorls of the frontal region. Until the hair-whorls of Mammalia have been more closely studied, it will not be possible to say what amount of significance should be assigned to this asymmetry. But it seems to me to offer an interesting field for enquiry.

As bearing on the question of the relative ages of the Brussels skull and our large hornless specimen, I may say that whilst the Brussels skull shows the molars and premolars in a worn condition and the incisors and canines much used, our larger skull has the following dental formula :—

Right side : i. $\frac{0}{3\text{ perm.}}$, c. $\frac{0}{1\text{ dec.}}$, pm. $\frac{2\text{ perm. (not cut), 1 dec.}}{3\text{ dec. (worn)}}$, m. $\frac{3\text{ perm. (in use)}}{3\text{ perm. (in use)}}$.

Left side : i. $\frac{0}{3\text{ perm.}}$, c. $\frac{0}{1\text{ dec.}}$, pm. and m. broken away above, same as right side below.

Our smaller skull has no lower jaw and shows three milk premolars and one permanent molar only, on each side of the upper jaw.

In conclusion, I may say that the adult dentition resembles, so far as the molars and premolars are concerned, very closely indeed that of *Giraffa*, whilst no new light is thrown by the new specimen on the permanent canines and incisors of which the larger of Sir Harry Johnston's specimens gave us full knowledge.

PLATE XXX.

PLATE XXX.

Two views of *Okapia johnstoni*, drawn from the skin obtained by Sir Harry Johnston as mounted in the Natural History Museum.

The specimen is not adult, but very nearly full-grown. The horns (recently discovered in specimens obtained by the Independent State of the Congo) are not yet developed. It is not known whether the specimen here figured is male or female.

P.J. Smit del. et lith.

Mintern Bros. imp.

THE OKAPI (OKAPIA JOHNSTONI)

PLATE XXXI.

PLATE XXXI.

Fig. 1. View from above of the smaller of the two skulls (that which does not belong to the skin). Drawn of about half the natural size. The actual measurement of the specimen is :—from the occipital margin to the free end of the nasals, 312 mm. ; from the occipital margin to the free end of the præmaxillaries, 375 mm.—Reference letters: *a*, supraorbital tumescence of the frontal bone (site of the future ossicusp or bony horn-core) ; *b*, the right præmaxillary bone ; *c*, the prælacrymal vacuity.

Fig. 2. View from above of the larger of the two skulls (that which belongs to the skin and lower jaw). Drawn of about half the natural size. The actual measurement of the specimen is :—from the occipital margin to the free end of the nasals, 375 mm.—Reference letters: *a*, supraorbital tumescence of the frontal bone (site of the future ossicusp or bony horn-core) ; *b*, the left præmaxillary, absent in the specimen and drawn here of a lighter tint ; *c*, the prælacrymal vacuity ; *d*, the median tumescence at the base of the nasal bones (see in this connection the profile view of the smaller skull in Plate XXXII.) ; *e*, the parietal bones ; the fronto-parietal suture is well-marked, but the interparietal suture is already obliterated in the smaller skull as well as in this ; *f*, the emarginated occipital ridge.

Fig. 3. The anterior group of teeth of the lower jaw belonging to the larger skull. The teeth are drawn as seen from above, and of the natural size. From the outer margin of the right canine to the outer margin of the left the measurement is 41 mm. The six incisors are those of the permanent set ; the canines are the deciduous ones, not yet replaced.—Reference letters: *dcl*, left deciduous canine ; *dcr*, right deciduous canine ; *pi*, *pi*, the six permanent incisors.

Fig. 4. The right permanent canine, obtained by cutting into the bone below the deciduous canine ; inner (adoral) face. One-tenth larger than natural size.

Fig. 5. Outer (aboral) face of the same tooth as that drawn in fig. 4.

Fig. 6. The left deciduous canine, drawn so as to show the outer (aboral) surface. One-tenth larger than natural size.

Fig. 7. Crown of anterior deciduous molar of the right lower series (marked dm^1) seen from above. Natural size.

Fig. 8. Crown of the second (counting the more anterior as the first) deciduous molar of the right lower series (marked dm^2) seen from above. Natural size.

Fig. 9. Crown of the third deciduous molar of the right lower series (marked dm^3) seen from above. Natural size.

Fig. 10. The crowns of the three non-successional or true molars of the right lower series seen from above : m^1, anterior true molar ; m^2, second true molar ; m^3, third true molar.

FIG. 1

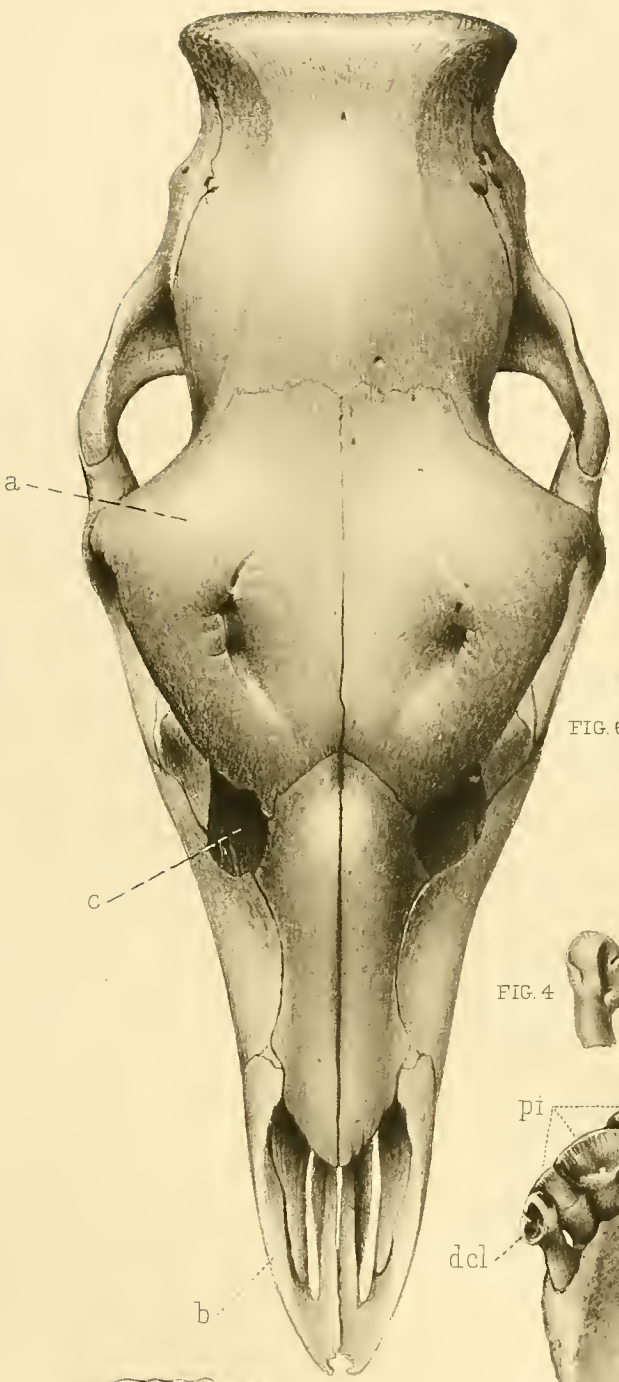


FIG. 2

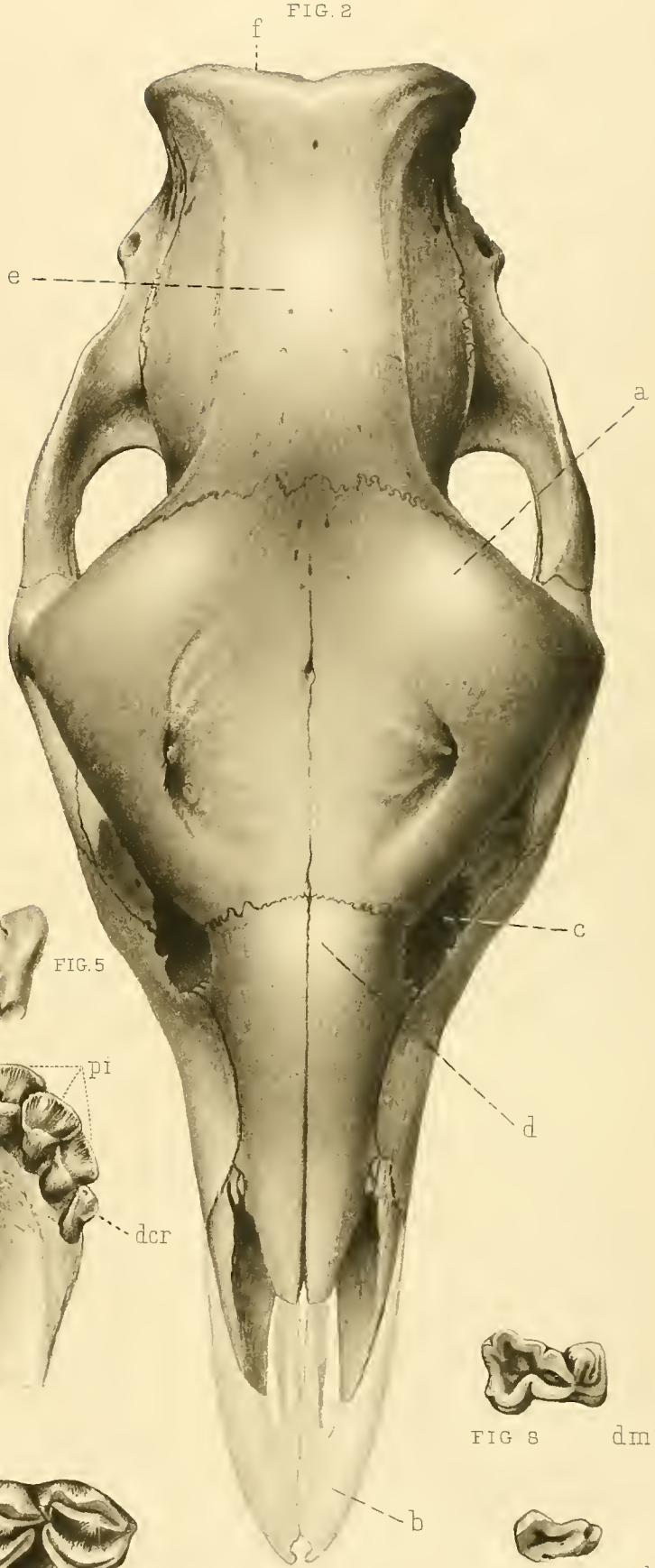


FIG. 6

FIG. 4 FIG. 5

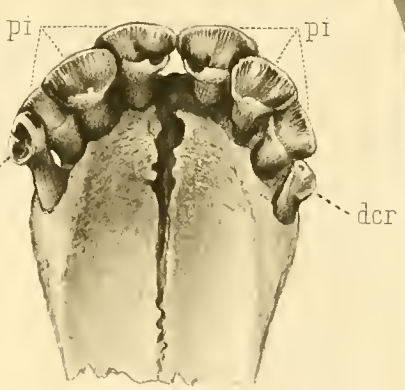


FIG. 3

dm^3

FIG. 9

FIG 8 dm^2

FIG. 7 dm^1

m^3

m^2

m^1

FIG. 10

THE OKAPI (OKAPIA JOHNSTONI)

Swan Electric Engraving

PLATE XXXII.

PLATE XXXII.

Fig. 11. View of the right side of the smaller skull drawn in fig. 1, Plate XXXI. The drawing is reduced to three-eighths of the natural size.—Reference letters: *a*, the supraorbital tumescence of the frontal bone (site of the future ossicusp or bony horn-core); *c*, the prælacrymal vacuity. The tumescence of the base of the nasal bones is well seen in profile.

Fig. 12. View of the right side and right ramus of the lower jaw of the larger of the two skulls, viz., that drawn in Plate XXXI. fig. 2. The drawing is reduced to three-eighths of the natural size. The basal part of the cranium is broken away in this as in the smaller skull, and the maxillary teeth of the right side only are preserved.—Reference letters: *a*, the supraorbital tumescence of the frontal bone; *b*, the absent præmaxillary bone, sketched in lightly of proportionate size from the same region of the smaller skull; *c*, the prælacrymal vacuity; *d*, the median tumescence of the base of the nasal bones; *e*, the parietal bone; *f*, the occipital crest; *y*, the three anterior incisors and canine of the lower jaw. The extremely small relative size of this group of teeth, as compared with the dimensions they exhibit in the Giraffe (and all other Pecora), should be realized by comparing this figure with the text-figure 12, representing the skull and lower jaw of a very young Giraffe, reduced to very nearly the same scale, that of the young Giraffe being one-ninth larger in scale.

Fig. 13. The molar teeth of the right upper series of the larger of Sir Harry Johnston's two skulls of Okapi, showing the crowns. The third true molar is broken and therefore not figured.—dm^1, the anterior milk-molar, not yet shed; pm^2, the second premolar, exposed by the shedding of the second deciduous molar, but not yet "cut"; pm^3, the third premolar, exposed by the shedding of the third deciduous molar, but not yet cut; m^1, anterior or first true molar (cut); m^2, second true molar (cut).

Fig. 14. The molar teeth of the right upper series of the smaller skull of the Okapi.—dm^1, dm^2, dm^3, the three deciduous molars; m^1, the first true molar. The second true molar had been cut, but is not preserved in the specimen; the third true molar had not yet been cut.

FIG. 11

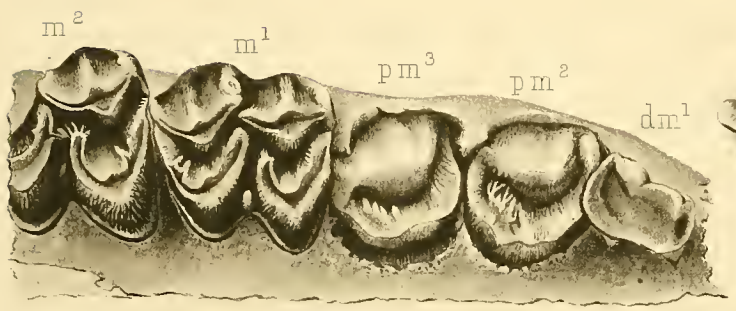


FIG. 13

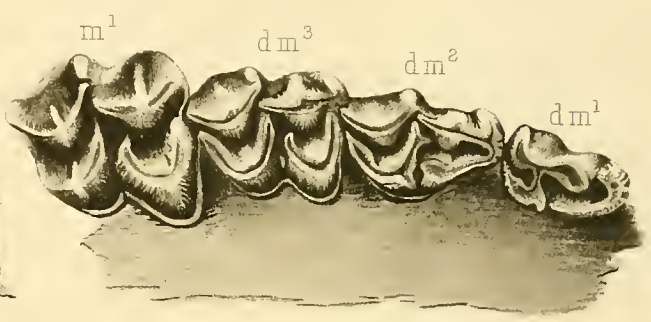


FIG. 14

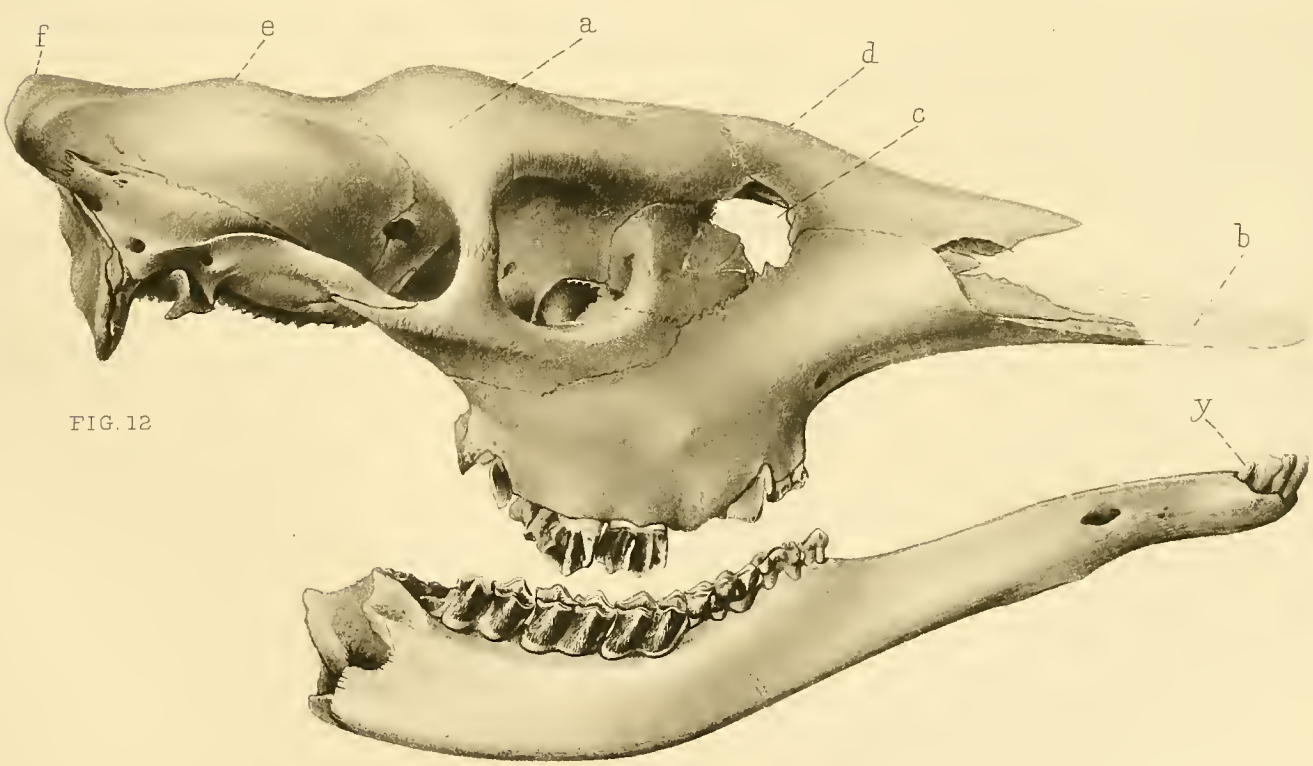


FIG. 12

THE OKAPI (OKAPIA JOHNSTONI)

H. Grönvold, del.

Swan Electric Engraving C°

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

(*continued*).

	To Fellows. £ s. d.	To the Public. £ s. d.
VOLUME XIV. (1896–1898, containing 47 Plates) .	Price 5 5 0	7 0 0
Part 1. (1896, containing 2 Plates)	„ 0 6 0	0 8 0
„ 2. (1896, containing 6 Plates)	„ 0 9 0	0 12 0
„ 3. (1897, containing 9 Plates)	„ 0 15 9	1 1 0
„ 4. (1897, containing 10 Plates)	„ 1 10 0	2 0 0
„ 5. (1898, containing 2 Plates)	„ 0 6 0	0 8 0
„ 6. (1898, containing 7 Plates)	„ 0 18 0	1 4 0
„ 7. (1898, containing 6 Plates)	„ 0 11 3	0 15 0
„ 8. (1898, containing 5 Plates and Title and Index)	„ 0 9 0	0 12 0
VOLUME XV. (1898–1901, containing 52 Plates) .	Price 5 15 6	7 14 0
Part 1. (1898, containing 8 Plates)	„ 0 15 9	1 1 0
„ 2. (1899, containing 5 Plates)	„ 0 9 0	0 12 0
„ 3. (1899, containing 4 Plates)	„ 0 9 0	0 12 0
„ 4. (1899, containing 4 Plates)	„ 0 9 0	0 12 0
„ 5. (1900, containing 24 Plates)	„ 2 12 6	3 10 0
„ 6. (1901, containing 4 Plates)	„ 0 11 3	0 15 0
„ 7. (1901, containing 3 Plates and Title and Index)	„ 0 9 0	0 12 0
VOLUME XVI.		
Part 1. (1901, containing 6 Plates)	Price 0 18 0	1 4 0
„ 2. (1901, containing 5 Plates)	„ 0 11 3	0 15 0
„ 3. (1901, containing 9 Plates)	„ 0 15 9	1 1 0
„ 4. (1902, containing 5 Plates)	„ 0 9 0	0 12 0
„ 5. (1902, containing 4 Plates)	„ 0 11 3	0 15 0*
„ 6. (1902, containing 3 Plates)	„ 0 15 9	1 1 0

* Part 5 of Vol. XVI., containing Mr. Mudge's paper on the Myology of the Tongue of Parrots, is not yet ready, and will be issued subsequently.—*August 1st*, 1902.

CONTENTS.

VII. *On* Okapia, *a new Genus of* Giraffidæ, *from Central Africa. By* E. Ray Lankester, *M.A., LL.D., F.R.S., F.Z.S., Director of the Natural History Departments of the British Museum, Correspondent of the Institute of France.* (Plates XXX.–XXXII.) . . . . . page 279

THE PUBLICATIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

The scientific publications of the Zoological Society of London are of two kinds—"Proceedings," published in an octavo form, and "Transactions," in quarto.

According to the present arrangements, the "Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the "Proceedings" by the Committee of Publication. A large number of coloured plates and engravings are attached to each annual volume of the "Proceedings," to illustrate the new or otherwise remarkable species of animals described in them. Among such illustrations, figures of the new or rare species acquired in a living state for the Society's Gardens are often given.

The "Proceedings" for each year are issued in four parts, on the first of the months of June, August, October, and April, the part published in April completing the volume for the last half of the preceding year. Commencing from January 1901 they form two half-yearly volumes.

The "Transactions" contain such of the more important communications made to the scientific meetings of the Society as, on account of the nature of the plates required to illustrate them, are better adapted for publication in the quarto form. They are issued at irregular intervals.

Fellows and Corresponding Members, upon payment of a Subscription of £1 1*s.* before the day of the Anniversary Meeting in each year, are entitled to receive all the Society's Publications for the year. They are likewise entitled to purchase the Publications of the Society at 25 per cent. less than the price charged for them to the Public. A further reduction of 25 per cent. is made upon purchases of Publications issued prior to 1871, if they exceed the value of five pounds.

Fellows also have the privilege of subscribing to the Annual Volume of the 'Zoological Record' for a sum of £1 (which includes delivery in the United Kingdom *only*), but this privilege only holds good if the subscription is paid before the First of December in each year.

Such of these publications as are in stock may be obtained at the Society's Office (3 Hanover Square, W.), at Messrs. Longmans', the Society's publishers (Paternoster Row, E.C.), or through any bookseller.

August, 1902.

P. L. SCLATER,
Secretary.

TRANSACTIONS

OF

THE ZOOLOGICAL SOCIETY OF LONDON.

VOL. XVI.—PART 7.

LONDON:

PRINTED FOR THE SOCIETY,

SOLD AT THEIR HOUSE IN HANOVER-SQUARE;

AND BY MESSRS. LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

October 1902.

Price 15*s*.

Taylor and Francis, Printers,] [Red Lion Court, Fleet Street.

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

	To Fellows. £	s.	d.	To the Public. £	s.	d.
VOLUME I. (1833–1835, containing 59 Plates) . . Price	3	13	6	4	18	0*
VOLUME II. (1835–1841, containing 71 Plates) . . „	4	0	0	5	6	6*
VOLUME III. (1842–1849, containing 63 Plates) . . „	3	8	3	4	11	0*
VOLUME IV. (1851–1862, containing 77 Plates) . . „	6	2	0	8	2	6†
VOLUME V. (1862–1866, containing 67 Plates) . . „	5	4	3	6	19	0†
VOLUME VI. (1866–1869, containing 92 Plates) . . „	11	5	0	15	0	0†
VOLUME VII. (1869–1872, containing 73 Plates) . . „	10	4	0	13	12	0†
VOLUME VIII. (1872–1874, containing 82 Plates) . . „	9	8	3	12	11	0†
VOLUME IX. (1875–1877, containing 99 Plates) . . „	12	1	6	16	2	0†
VOLUME X. (1877–1879, containing 95 Plates) . . „	10	0	3	13	7	0†
GENERAL INDEX, Vols. I. to X. (1833–1879) . „	0	7	6	0	10	0
VOLUME XI. (1880–1885, containing 97 Plates) . . „	9	12	0	12	16	0
VOLUME XII. (1886–1890, containing 65 Plates) . . „	5	8	0	7	4	0
VOLUME XIII. (1891–1895, containing 62 Plates) . . „	6	8	3	8	11	0

* No copies of these volumes remain in stock.

† Only complete copies of these volumes are left in stock.

Continued on page 3 of Wrapper.

VIII. *On the Structure of the Larval* Polypterus.

By J. S. Budgett, *M.A., F.Z.S.*

Received and read December 17, 1901.

[Plates XXXIII.–XXXV.]

Contents.

Page

I. Introduction 315
II. Material and Methods 317
III. The Skeleton 319
IV. Urinogenital Organs 330
V. Conclusion 338

I.—Introduction.

Although *Polypterus* is undoubtedly one of the most interesting forms of recent Vertebrata, in that it is one of the two survivors of a very ancient group of fishes which existed in an abundance of forms in the Devonian era, its anatomy was until recently only imperfectly known; while nothing was recorded of its life-history and development, the knowledge of which might be expected to throw much light on the relationships of the great groups of the lower Vertebrata. The study of the structure of a very young larval *Polypterus* which I had obtained seemed to me therefore of considerable interest.

The attempt to arrange recent groups of animals in a linear series or even in the form of a genealogical tree appears to me to be misleading. The affinities of recent groups should rather be represented by a chart of an archipelago of groups, the remains of a submerged continent, the configuration of which the study of palæontology alone can reveal.

The significance of the observations recorded in the following pages appears to me to be that *Polypterus* must be regarded as having affinities with several of the great groups of fishes on the one hand, and also with the amphibians on the other hand. From this I am led to conclude not that the modern Crossopterygians form a connecting-link in a phylogenetic sense, but rather that they form a central group amongst recent forms having affinities with, and so connecting together, a number of the great groups of Vertebrates; for, as will be seen, in parts of their structure they show undoubted affinities with the Teleostei and Ganoidei, while in other respects their structure reveals affinities with the Elasmobranchii; in addition, however, they show affinities in a third direction, namely with the Stegocephali and through them to the Amphibia. That there is any very close connection between the living Crossopterygians and the living Dipnoi does not appear to be the case.

Some authors have attempted to show that the Amphibia may have been directly derived from some such forms as the recent Crossopterygii, others derive them from the Dipnoi: with both these views I venture to disagree. The Devonian Crossopterygii no doubt merged into the Devonian Dipnoi, and it was from forms probably intermediate between the Crossopterygii and the Dipnoi that the ancestral Amphibians originated. In these times likewise the Crossopterygii merged into the Elasmobranchii and thirdly into the Ganoidei, and it was from forms probably intermediate between the Crossopterygii and the Ganoidei that the Teleostei originated.

Thus the Amphibia appear to be related to the Elasmobranchii in two ways—first through the Dipnoi, second through the Crossopterygii. In like manner, the

Text-fig. 1.

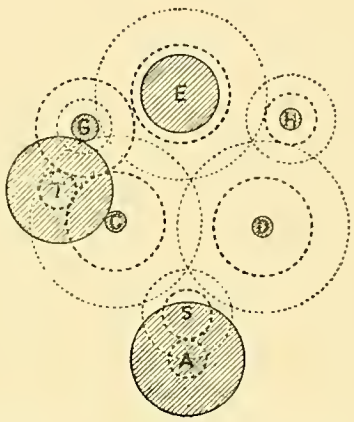


Diagram to illustrate the affinities of Vertebrata and their relative importance in Primary, Secondary, and Tertiary times.

A. Amphibia and Amniota.
C. Crossopterygii.
D. Dipnoi.
E. Elasmobranchii.
G. Ganoidei.
H. Holocephali.
S. Stegocephali.
T. Teleostei.

Primary.
Secondary.
Tertiary.

Teleostei are related to the Elasmobranchii in two ways, the Crossopterygii and the Ganoidei.

To attempt to give a definite chart of the Ichthyopsida would be to assume a perfect knowledge of the structure, development, and palæontology of the various groups which I do not pretend to possess. I will therefore give a mere diagram (text-fig. 1) in order to illustrate my meaning, and pass on to the facts of development as observed

in this larval Crossopterygian, attempting such interpretation as they seem to warrant, in view of the absence of knowledge of the early stages in its development.

II.—Material.

The external features of the larva of *Polypterus*, which forms the subject of this paper, I have described in a former paper [1]. I have had at my disposal only a single specimen, measuring 30 mm., obtained during a collecting-trip to the Gambia in 1900 [2]. In the present paper I have given an account of the structure of the cartilaginous skeleton in this larva, and somewhat of its subsequent development as studied in a number of specimens measuring from 9 cm. upwards. I have also given an account of the genital and excretory system of organs in this small larva, the subsequent development of which I have already described in a previous paper [3].

It will be seen that between the stage of this small larva (30 mm. in length) and the next stage at my disposal (namely, specimens 9 cm. in length) there is a considerable gap. As regards the study of the development of the skeleton, this is of no importance, as the intervening stages are easily interpreted. As regards the development of the genital ducts, however, an intermediate stage, between that here described and that of the 9 cm. larva already described, is much to be desired. Of the developmental stages of *Polypterus* preceding that here described hitherto nothing has been observed.

It may be said of this larva that it exhibits the condition of the last of the series of changes which is undergone by *Polypterus* in its development from the egg before it assumes the external appearances of the adult form. The term "larva" has frequently been employed for young *Polypteri* of all sizes which retain the external larval gill; but as this gill is retained frequently by adult specimens of some species of *Polypterus*, it is in no way justifiable to term such specimens as happen to possess this organ "larvæ," irrespective of their being in a larval condition otherwise.

I have laid some stress upon this, as an account of the excretory system of a *larval Calamoichthys* has been published, in which I am sure that the author has been influenced in his description by the supposition that the specimen was in a larval condition, though measuring 12 cm. in length. But to this I shall return later.

Methods.

The larva, which had been preserved in 5 per cent. formalin, was cut into transverse sections, of which the anterior half were 10 μ in thickness, while the posterior half were 7 μ thick. They were doubly stained with hæmatoxyline and eosine. All the

[1] Trans. Zool. Soc. London, vol. xvi. p. 118.

[2] In the account of the external features, this larva was said to be of *Polypterus lapradii*. It has recently been shown by Mr. Boulenger that the larva is that of *P. senegalus* and not that of *P. lapradii*.

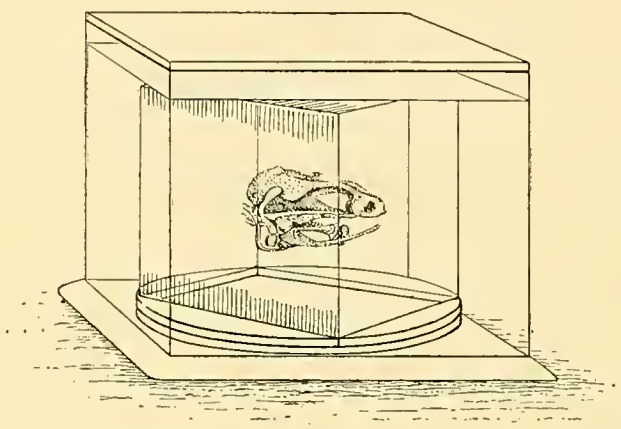
[3] Trans. Zool. Soc. London, vol. xv. p. 323.

figures of Plate XXXIII., and figs. 9 and 10 of Plate XXXIV., were drawn from reconstructions by Kerr's method; that is, the sections were drawn on sheets of ground-glass by the aid of the camera lucida and a medium, of the same refractive index as the glass, run in between the sheets of glass [1].

I have found it extremely convenient to use this method in the following way:— Five dozen sheets of ground-glass 4 inches square and $\frac{1}{16}$ inch thick are ground and polished *en masse*, so that their cut edges when placed together form plain surfaces.

After having drawn the first section, the image of the second section is exactly superimposed on the drawing of the first, which is then removed, and the next glass plate being put exactly in its place and the drawing having been made the image of

Text-fig. 2.



Apparatus used in reconstructing.

the third section is exactly superimposed on the drawing of the second, and so on. In this way all the successive sections have the same register as the first, and when placed together in the form of a cube the magnified image of the object is formed.

The cube of glass plates is then transferred plate by plate to a cubical glass jar, the width of which is a little more than the diagonal of the plates, so that the cube of glass can just freely rotate within the square vessel. The vessel contains a mixture of fennel-oil and oil of cedar, which I have found to be sufficiently near the refractive index of the glass, and to have the advantage over clove-oil that it does not become dark with age.

The cube of plates is held in position by means of the glass turn-table shown in text-fig. 2. It consists of a circular disc of plate-glass, the diameter of which is very

[1] Quart. Journ. Micr. Science, vol. xlv. pt. 1, p. 6.

slightly less than the width of the vessel, so that it can rotate freely on the bottom of the vessel. A second and similar disc of glass has four segments cut off it in such a way that when placed together and cemented to the first disc, so that their circumferences coincide, there is formed a trough which will exactly carry the cube of glass plates.

If they fit properly the plates must stand vertically, and the cube of plates can be rotated on the turn-table so that the reconstructed image can be seen from any aspect by an observer always looking normally at the surface of the fluid, *i. e.* the side of the square vessel.

No image, of course, can be seen when the cube is so turned that the observer looks between the surfaces of the plates, but with a very slight turning from this position the image at once comes into view.

If it is desired to reconstruct only a small series of sections, the remainder of the cube can conveniently be made up of squares of thick plate-glass (see text-fig. 2) in place of thin mat-surface squares.

III.—The Skeleton.

The Chondrocranium.—The cranial anatomy of the adult *Polypterus* has been made known by Traquair [1], while that of the half-grown *Polypterus* was described by Pollard [2].

In this small larva, measuring 30 mm., there is as yet but slight traces of ossification, and that only in the membrane-bones of the head. The primordial cartilaginous cranium may therefore be said to be at the height of its development.

The auditory capsule, though fused with the occipital and parietal region of the cranium anteriorly, posteriorly is separated from the exoccipital region by a very large foramen, giving exit to the xth and xith cranial nerves (Pl. XXXIII. fig. 4, X., XI.). From this foramen a fissure extends between the auditory capsule and the supraoccipital region, and likewise a fissure between the auditory capsule and the basioccipital region. The exoccipital cartilage, though fused dorsally with the supra- and ventrally with the basioccipital regions, is yet easy to recognize as a neural arch, which is becoming fused with the cranium (Pl. XXXIII. fig. 4, *Ex.occ.*). The base of this neural arch has the same form and position as the base of the first true neural arch of the vertebral column, in front of which the first spinal nerve has exit (Pl. XXXIII. fig. 4, *Sp.i.*).

The basioccipital region does not completely envelop the anterior end of the notochord, but is composed of two halves (the parachordal cartilages) abutting on the two sides of the front end of this structure (Pl. XXXIII. fig. 2). Posteriorly

[1] Journ. Anat. & Phys. vol. v. (1871).

[2] Zool. Jahrb. Anat. u. Ont. Bd. v. (1892).

these two lateral masses of cartilage send wings ventrally, which meet and fuse below the dorsal aorta, enclosing it in a short canal which is roofed in by the notochord itself (Pl. XXXIII. figs. 2 & 4, *s.A.br.*). Anteriorly to the bifurcation of the aorta, the basioccipital cartilages fuse below the notochord, sending forward a median narrow plate of cartilage which underlies the tip of the notochord (Pl. XXXIII. fig. 3, *s.Ch.br.*). The fused auditory supra- and basioccipital regions form on either side an exceedingly massive cranial wall. These walls are united dorsally by a fairly solid bridge of cartilage of shortest extent antero-posteriorly in the middle line (Pl. XXXIII. fig. 2, *s.oc.br.*). Ventrally, however, they are only connected by the two little bridges of cartilage already mentioned—the one passing underneath the dorsal aorta behind its bifurcation, the other below the tip of the notochord in front of the bifurcation of the aorta.

In front of the tip of the notochord the floor of the cranium is formed merely of membrane, the bases of the lateral walls of the cranium being widely separated by a very large fontanelle in the posterior region of which lies the hypophysis [1]. The hypophysis is not at this stage enclosed in a special pocket of the cranial wall or "sella turcica," but curving backwards lies close under the hind end of the mid-brain (separated from it by thin membrane) and above the dermis of the roof of the mouth. In a 9 cm. specimen the glandular part of the hypophysis is much larger in proportion and the membrane separating the hypophysis from the floor of the mid-brain has been converted into cartilage of considerable thickness, while the special cavity so formed remains in communication with the rest of the cranium by the opening for the passage of the infundibulum.

On the dorsal surface of the auditory region there extends forwards from the anterior end of the fissure separating the supraoccipital region from the posterior end of the auditory capsule a fairly pronounced ridge. On the lateral surface, along the line of the horizontal semicircular canal, there is a very pronounced pterotic ridge bearing in its middle portion the articulatory surface for the head of the hyomandibular cartilage (Pl. XXXIII. figs. 1, 2, & 3, *Pt.r.*). The front portion of this ridge gives off the sphenotic wing, which separating from the cranial wall passes forwards as a horizontally flattened bar of cartilage to fuse again with the cranial wall in the supraorbital region (Pl. XXXIII. figs. 1 & 3, *Sph.*).

[1] At this stage the glandular part of the hypophysis is very small and flattened against the dermis of the roof of the mouth; its tubules open anteriorly into a small cavity which is in communication with the mouth-cavity by a fairly wide duct, which persists until after the larva has grown to 9 cm. in length. According to Bickford (Anatomische Anzeiger, Bd. x. p. 469), this duct remains permanently open in *Calamoichthys*. The nervous portion of the hypophysis has a very wide lumen and passing backwards ends in five finger-like processes. In the 9 cm. specimen these have branched and become mingled with the tubules of the glandular portion posteriorly, but do not appear to be continued into them as stated by Waldschmidt (Anatomische Anzeiger, Bd. ii. p. 318).

On the ventral surface of the auditory region of the cranium, from the point in the middle line where the aorta bifurcates, on either side there extends forwards and outwards a deep groove in which runs the branch of the aorta, being the efferent artery from the hyoid external gill, and receiving a small branch from the first branchial arch.

Anterior to the bridge of cartilage uniting dorsally the two lateral masses of cartilage of the auditory region, the roof of the cranium is formed entirely of membrane to the front end of the cranial cavity, except for a delicate but continuous bridge of cartilage in the region of the pineal body (Pl. XXXIII. figs. 1 & 3, *Ep.br.*). This slender bridge expands towards the middle line into a horseshoe-shaped plate (Pl. XXXIV. fig. 1, *Ep.br.*) lying over the vesicle of the third ventricle [1]. The pineal gland itself lies in the centre of the horseshoe, and is not covered by cartilage but lies in the dermis of the skin (Pl. XXXIV. fig. 1, *Ep.*).

The lateral walls of the cranium extend forward from the auditory region on either side of the alisphenoid region as continuous vertical plates of cartilage, somewhat dumbbell-shaped in section and perforated by foramina for the iiird, vth, and viith nerves in the thinner middle portion (Pl. XXXIII. fig. 1, III., V., VII.). In the sphenethmoid region there is a large lateral fontanelle closed only by membrane through which passes the optic nerve, while above and below this membranous portion there pass the thickened upper and lower cartilaginous borders of the cranial wall, connecting on either side the ethmoidal region with the posterior region of the cranium (Pl. XXXIII. figs. 1 & 3). A section therefore passing through the middle of the orbital region cuts merely four bars of cartilages—two supraorbital bars separated from one another by a wide superior fontanelle, and two infraorbital bars (trabeculæ cranii) separated by a wide inferior fontanelle, the upper and lower of each side being separated by the large lateral fontanelle; the greater part of the "sphenethmoid" bone of *Polypterus* is therefore not preformed in cartilage.

In this region the section of the supraorbital bar of cartilage is **V**-shaped; the outer limb of the **V** is the anterior prolongation of the sphenotic wing, which is here fused with the supraorbital bar (Pl. XXXIII. fig. 3, *Sph.*). In the angle thus formed lies the supraorbital canal of the lateral line system (Pl. XXXIV. fig. 1, *s.o.c.*). In front of the interorbital region the four bars of cartilage in the side walls of the cranial cavity expand and unite together, forming the anterior wall of the cranial cavity and being fused with the olfactory capsules (Pl. XXXIII. fig. 1). A canal for the passage of the olfactory branches of the vth and viith cranial nerves penetrates the

[1] This vesicle is called by Waldschmidt the "epiphysis cerebri (pineal gland)"; in reality, however, it is the homologue of the median vesicle of *Lepidosteus* described by Balfour and Parker (Phil. Trans. Roy. Soc. Lond. part ii. 1882). The epiphysis itself lies over and behind this vesicle, and was apparently not found by Waldschmidt in *Polypterus* (loc. cit.).

outer portion of the supraorbital bar of cartilage at the point where it is fused with the olfactory capsule (Pl. XXXIII. fig. 1, *f.ol.*). Just anterior to this the capsule itself is penetrated by the same nerve. The olfactory capsules are very large and thin-walled, oval-shaped, and perforated anteriorly by a crescent-shaped nasal aperture (Pl. XXXIII. fig. 1). They are separated from one another to some extent anteriorly by a deep groove which ends above a spade-shaped rostral prolongation of the ventral portion of the nasal septum.

The ventral side of the olfactory capsule bears a facet for the articulation of the anterior end of the palato-quadrate bar of cartilage (Pl. XXXIII. fig. 1, *P.Qu.art.*).

The general form of the primordial cranium at this stage resembles very much that of the Selachii, especially the Scylliidæ, but in the absence of cartilage in the middle portion of the cranial walls, and the size of the great fontanelle, there is some similarity to the Urodela. The bridge of cartilage across the supracranial fontanelle seems to indicate a former roofing of the cranial cavity by cartilage, for, later, this bridge is represented by the small plate of cartilage noted by Pollard, and finally disappears. The absence of cartilage immediately over the pineal gland seems to indicate that the cranial roof was formerly perforated by a parietal foramen.

The Visceral Arches.—The *palatoquadrate bar* is a pyramidal mass of cartilage, the anterior corner of which is drawn out into a vertically flattened bar, which anteriorly becomes almost circular in section, and finally flattened horizontally to form the articulation with the facet on the ventral side of the nasal capsule (Pl. XXXIII. fig. 1, *P.Qu.art.*). The quadrato-mandibular articulation is saddle-shaped, and it is in the region of this articulation that the palato-quadrate bar has its greatest transverse diameter (Pl. XXXIII. figs. 1, 2, 3, *P.Qu.*, *Mk.*).

Behind this articulation the bar narrows to a point, which is concave vertically. This concavity rests upon the lower limb of the hyomandibular cartilage. The palato-quadrate bar receives no direct support from the cranial wall; the articulation is therefore hyostylic.

The *mandibular bar* has a similar pyramidal shape posteriorly, while its anterior portion forms a more regularly cylindrical rod than the palato-quadrate bar, and tapers to the symphysis with its fellow (Pl. XXXIII. figs. 1, 2, 3, *Mk.*).

The hyoidean arch, consisting of hyomandibular, stylohyal, ceratohyal, and hypohyal cartilages, articulates with the facet already mentioned on the underside of the lateral ridge of the auditory region (Pl. XXXIII. figs. 1, 2, 3, *Pt.r.*).

The *hyomandibular* consists of two rounded masses connected by a slender curved rod bearing upon its posterior convex surface the anterior end of a rod of cartilage segmented into two fairly equal portions, which constitute the skeletal axis of the base of the external gill (Pl. XXXIII. figs. 1, 2, 3, *Op.*). This rod persists as the small nodule of cartilage on the inner side of the opercular bone, which has been before noted by Van Wijhe and Traquair.

The *stylohyal* (Pl. XXXIII. figs. 1, 2, *St.Hy.*) is a rounded mass of cartilage which takes no part in the suspension of the jaws.

The *ceratohyal* (Pl. XXXIII. figs. 1, 2, 3, *C.Hy.*) is massive at either end, but constricted to a narrow bar in its middle portion.

The *hypohyal* (Pl. XXXIII. figs. 1, 2, 3, *H.Hy.*) is an almost spherical cartilage connecting the front end of the ceratohyal with that of the 1st branchial bar.

The *basibranchial* (Pl. XXXIII. figs. 2, 3, *B.Br.*) is a massive median cartilage on either side of which are articulated the enlarged lower ends of the four branchial bars. Each of these bars, in passing backwards and upwards, becomes very slender. Posteriorly these become slightly thickened again and curve inwards; finally the upper end of the first branchial abuts upon the cranial wall just below the articulation of the hyomandibular, while the 2nd, 3rd, and 4th branchials tapering, curve downwards and end freely close under the auditory capsule (Pl. XXXIII. figs. 1, 2, 3, *Br.* 1, 2, 3, & 4).

Between the palatoquadrate and mandibular cartilage there lies a crescent-shaped labial cartilage with its convex surface forwards, the upper horn being more slender than the lower (Pl. XXXIII. figs. 1, 3, *Lb.*).

In the arrangement of the cartilages of the suspensorial apparatus the larval *Polypterus* exhibits a condition exactly intermediate between that of the hyostylic Selachians and the Teleostei, there being no very intimate union between the palatoquadrate and hyomandibular cartilage by means of a symplectic cartilage corresponding to that of Teleostei. The general correspondence of the arrangement with that of the larval Salmon on the one hand and the hyostylic Selachii on the other, and the relation of the spiracle to the hyomandibular in *Polypterus*, seem to me to go a long way towards dispelling doubts as to the homology of the suspensorium of the Teleostei with that of the hyostylic Selachii, such as have been entertained by some authors[1]. In this particular of course *Polypterus* differs widely from all living Amphibia, where the palatoquadrate bar has become fused with the cranial wall and the hyomandibular usually reduced.

On the other hand, the presence on the hyomandibular of *Polypterus* of a segmented rod of cartilage supporting the external gill is paralleled in the Aistopodous Stegocephali; for in *Dolichosoma longissimum*, according to Fritsch[2], there is found attached to the hyoid arch a skeletal structure which apparently supported an external gill. It is difficult, however, to make out whether this structure was attached to the periotic portion of the skull itself or to the upper end of the hyoid arch.

[1] See H. B. Pollard, "The Suspension of the Jaws in Fish," Anatomische Anzeiger, x. p. 17. Also Parker and Haswell, 'Text-book of Zoology,' vol. ii. p. 202.

[2] Fauna der Gaskohle und der Kalksteine der Permformation Böhmens.

The Vertebral Column.

The *notochord* is at this stage of even calibre throughout the greater part of its length, tapering suddenly, however, anteriorly and gradually posteriorly towards its termination, where it shows a slight upward tendency (Pl. XXXIII. figs. 4, 5, 6, *Ch.*).

The structure of the notochord in *Polypterus* is very similar to that of *Lepidosteus* and the Teleosteans. The meshes between the large vacuoles enclose here and there a nucleus. The vacuoles towards the sheath become smaller and the nuclei more numerous, and pass rather suddenly into a definite nucleated epithelium lining the sheath of the notochord (Pl. XXXIV. fig. 10, *Ch.ep.*). The sheath itself is very thick and almost structureless, being from $\frac{1}{10}$ to $\frac{1}{12}$ the thickness of the diameter of the vacuolated portion of notochord. A very delicate membrana elastica bounds the sheath externally (Pl. XXXIV. fig. 10, *m.el.e.*) and separates it from the connective tissue surrounding the notochord with which the septa between the muscles are continuous.

At the junction of these septa with the notochordal sheath are found on either side three metameric series of cartilages—a dorsal row of stout pyramidal masses forming the bases of the neural arches with which they are continuous (Pl. XXXIII. figs. 4, 5, 6, & Pl. XXXIV. fig. 2, *n.pr.*); a lateral row of small pyramidal masses forming the foundations for the transverse processes and lateral ribs (Pl. XXXIII. figs. 4, 5, & Pl. XXXIV. fig. 2, *l.pr.*); and the ventral row of still smaller nodules forming the foundations of the ventral series of ribs (Pl. XXXIII. figs. 4, 5, 6, & Pl. XXXIV. figs. 2 & 10, *v.pr.*).

All these cartilages rest directly on the notochordal sheath, and in each metamere the three masses lie in nearly the same transverse plane, so that one section often passes through all three structures.

Neither the pyramidal bases nor their neural prolongations are fused across the mid-line, except in the tail-region. The bases are quite separate, while the upper ends of the two halves of the neural arch curve backwards, come into close contact with one another, and carry the lower end of the median dorsal spine (Pl. XXXIII. figs. 4, 5, 6, *d.sp.*).

In the anterior region of the vertebral column all three series are well-developed. In this region the lateral series are continued outwards along the septa, between the dorso-lateral and the ventro-lateral muscles, forming complete rib-like structures (Pl. XXXIII. fig. 4, *l.pr.*).

The ventral series are also well-developed and pass outwards between the ventro-lateral muscles and the kidneys (Pl. XXXIII. fig. 4, & Pl. XXXIV. figs. 2 & 10, *v.pr.*). At this stage they do not in the anterior region reach the peritoneum.

In a section passing between the myomeres, and therefore through the bases of these cartilages, somewhat further back, it may be seen that the section cuts small nodules of cartilage at the extremity of the septa between the dorso-lateral and ventro-lateral muscles (Pl. XXXIV. fig. 2, *o.l.r.c.*). These outer nodules lying near the nerve of the lateral line are not, however, connected with the cartilage of the central end of the septum. That is to say, the cartilage which forms the basis of the outer portion of the lateral ribs is developed independently of the cartilaginous basis of the transverse process.

In the middle region of the vertebral column both the lateral and ventral cartilages are small, while the dorsal cartilages of the two sides are seen to be placed in a slightly alternating position, so that a transverse section passing through the centre of a dorsal cartilage on the right side will pass through the posterior fringe of the dorsal cartilage of the left side (Pl. XXXIII. fig. 5, *n.pr.*).

In the caudal region the lateral series of cartilages are not found, while the ventral cartilages, though retaining their position, become the greatly enlarged hæmal arches. The first pair of enlarged ventral cartilages, however, do not unite ventrally, but each half bears at its extremity one of the last two interspinous cartilages of the anal fin [1] (Pl. XXXIII. fig. 6, *l.v.pr.*, *r.v.pr.*). The two preceding interspinous cartilages of the anal fin are borne by similar rods of cartilage, which, however, do not unite with the ventral cartilage.

The most anterior cartilage of the anal fin is somewhat expanded antero-posteriorly, but is not supported by the hæmal cartilage.

Behind the anal fin the right and left ventral cartilages fuse together below the hæmal canal to form rod-shaped median cartilages, which expand distally and support directly the rays of the ventral fin of the diphycercal tail of *Polypterus* (Pl. XXXIII. fig. 6, *h.c.*).

In this region the right and left halves of the neural arches fuse together to form the dorsal spines (Pl. XXXIII. fig. 6, *d.sp.*), while wedged in between these are found the interspinous processes, which, expanding distally to trumpet-shaped masses of cartilage, support the rays of the dorsal fin of the tail. There is no correspondence between the dorsal spines of the neural arches and these interspinous processes, for there may be one, two, or three of the latter intervening between two of the former. More anteriorly these interspinous processes become much reduced and do not penetrate between the dorsal spines. As the extremity of the tail is reached the neural and

[1] I have satisfied myself that my description of the way in which the anal fin is supported in this specimen is correct, but I am not quite sure that this will be found to be the normal arrangement. It seems, at any rate to me, to be an additional proof that the hæmal arches are formed from the bending downwards and uniting of originally separate ventral ribs, which have secondarily assumed the function of supporting the anal fin.

hæmal arches, together with the interspinous processes of the dorsal fin, become more and more oblique, lying almost parallel to the notochord (Pl. XXXIII. fig. 6, *d.sp.*, *l.sp.*). Finally there lies upon the dorsal, and also upon the ventral, side of the notochord a flattened mass of cartilage, which appears to be composed of the rudiments of several neural and hæmal arches (Pl. XXXIII. fig. 6, *f.n.pr.*, *f.v.pr.*). The notochord extends beyond this incomplete cartilaginous tube, a bare filament embedded in the fin-rays of the tail.

At this stage there is no trace of any intervertebral cartilages, neither is there any trace of a ring of cartilage enclosing the intervertebral regions of the notochord.

In older specimens of 9 cm. length considerable deposits of bone have appeared, producing important changes in the structure of the vertebral column and its processes.

In the vertebral regions the cartilaginous bases of the neural arches and lateral processes are still seen, though now surrounded by bone, deposited in the connective tissue adjoining the notochord (Pl. XXXIV. figs. 3, 4, 8, *n.pr.*, *l.pr.*). The ventral cartilages have disappeared from the neighbourhood of the notochord. The bony deposits which have enclosed the lateral cartilages and formed the transverse processes have caused the proximal ends of the ventral cartilages to recede outwards, and these are now found attached loosely to the underside of the transverse processes below their attachment to the lateral bony ribs, which have now become formed in the connective tissue of the septa between the dorso-lateral and ventro-lateral muscles (Pl. XXXIV. figs. 3, 4, 7, *tr.pr.*). The ventral cartilages themselves form the heads of the ventral bony ribs which have now become formed at the junction of the septa between the successive ventro-lateral muscles with the peritoneum (Pl. XXXIV. figs. 4, 7, *v.pr.*).

The shifting outwards of the heads of the ventral ribs or hæmal arches with the development of the large transverse bony processes of the vertebræ has resulted in allowing space for the greatly enlarged kidneys.

It will be seen that the heads of these ventral ribs do not now lie quite in the same transverse plane as the transverse processes, but crossing them diagonally project towards the muscles in front of the transverse processes (Pl. XXXIV. fig. 7). In the full-grown *Polypterus* the heads of the ventral ribs articulate with the intervertebral regions of the vertebral column, that is, between two successive vertebræ, and it might be thought that this was their original place of attachment. It will, however, be understood, from the above description of their mode of growth, that they are originally attached to the ventral surface of the notochord in the same transverse plane as the bases of the transverse processes, that is, *vertebral* in position, and that they later lose their connection with the notochord, become twisted across the ends of the transverse processes, and with the subsequent development of the bony centra become attached again to the vertebral axis, and are finally *intervertebral* in position.

The centra themselves are at this stage very thin and hourglass-shaped, expanding widely anteriorly and posteriorly; they are not formed previously in cartilage (Pl. XXXIV. fig. 8, *c.*) except for the small neural and lateral cartilages which they enclose; they directly surround the chordal sheath. There is, however, a single layer of cells separating them from the latter in the position where the membrana elastica externa should be, which somewhat resemble cartilage-cells; they do not, however, stain in the very characteristic way in which all other cartilage in this specimen has stained (Pl. XXXIV. fig. 6, *m.c.*). The cartilages of the neural arches play but a very small part in the formation of the bony neural arches, which are also formed directly in connective tissue.

In specimens 13 cm. long the vacuolated portion of the notochord has become constricted vertebrally, while the sheath of the notochord, retaining a considerable thickness in the vertebral region, intervertebrally becomes greatly thickened (Pl. XXXIV. fig. 6, *Ch.sh.*). It is this thickening of the notochordal sheath which is the chief cause of the great expansion of the bony vertebræ in the intervertebral regions. At this stage all trace of cartilage has disappeared from the composition of the vertebræ (Pl. XXXIV. fig. 5).

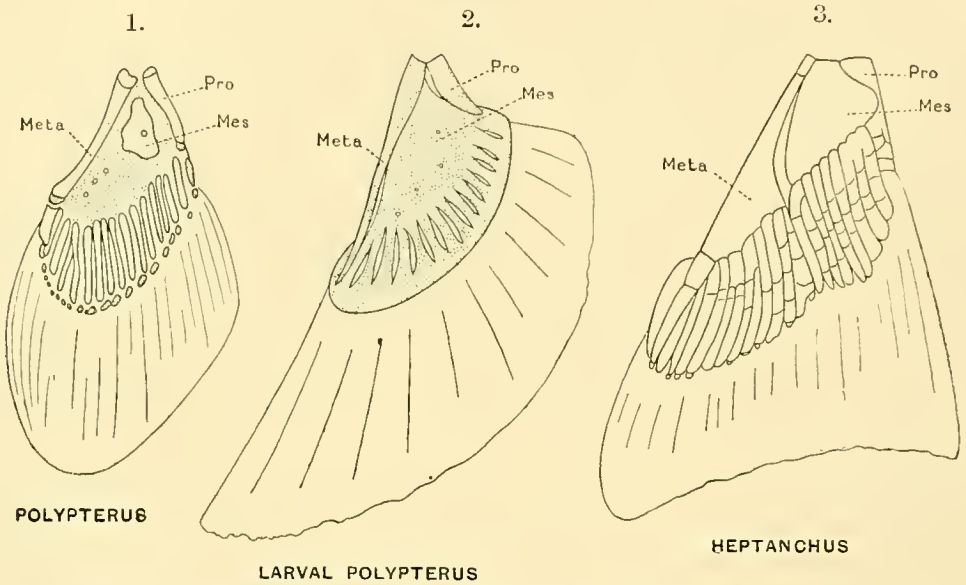
The formation of the vertebral centra in *Polypterus* is very much on the same lines as that of *Lepidosteus* and the Teleostei. It differs from *Lepidosteus* in the absence of the intervertebral rings of cartilage which give rise to the procœlous articulations in that form, and from *Amia* in the absence of intercalated cartilages. In the possession of three pairs of vertebrally placed cartilages resting upon the notochordal sheath before the commencement of bone formation, *Polypterus* differs from all living Vertebrates.

That *Polypterus* is provided with a double set of ribs has long been known; and by some authors the upper series has been homologized with the ribs of Elasmobranchii, Amphibia, and Amniota, and the lower series with the ribs of the Dipnoi, Ganoidei, and Teleostei. Göppert especially[1] has developed this view regarding the reduction of the lower series in the former groups as due to the suppression of the ventro-lateral muscles. The starting-point which Göppert took was the condition in *Calamoichthys* at the stage where the lower ribs are attached to the under sides of the upper ribs shown in Pl. XXXIV. fig. 4 of *Polypterus*. The discovery that all the lower ribs in *Polypterus* have their origin in a ventral series of cartilages resting directly on the notochordal sheath seems to me to very much strengthen his views. The absence of intercalated cartilages, such as are found in the majority of Vertebrates exclusive of the Teleostei or of the intervertebral cartilage-rings of *Lepidosteus*, may possibly be connected with the early and great development of membrane-bone which is so characteristic of the development of all the skeletal structures of *Polypterus*.

[1] Morph. Jahrb. Bd. xxiii.

The Shoulder-girdle and Pectoral Fins.—The cartilaginous shoulder-girdle consists of a compact mass of cartilage of considerable thickness anteriorly, and, though thinning out ventrally, of no great extent in a dorso-ventral direction (Pl. XXXIII. fig. 7). Posteriorly, it is prolonged as a thin plate of cartilage, towards the hinder border of which is the great coracoidal foramen (Pl. XXXIII. figs. 7 & 8, *Cor.f.*). Above this foramen is situated the protuberance bearing the convex facet which articulates with the proximal ends of the pro- and metapterygial cartilages of the pectoral fin. From behind, this protuberance appears as a distinct short rod of cartilage attached only at its proximal end to the flattened portion of the shoulder-girdle (Pl. XXXIII. fig. 7). In reality, however, it is continued forwards into the anterior thick portion of the girdle as a thickened ridge.

Text-fig. 3.



Skeleton of pectoral fin of *Polypterus* and *Heptanchus*.

Pectoral fin of—1. Adult *Polypterus*.
2. Larval „
3. *Heptanchus*.

Meta. Metapterygium. *Mes.* Mesopterygium. *Pro.* Propterygium.

The pectoral fin of *Polypterus* is one of its most characteristic features, being unlike that of all other Vertebrates excepting its congener *Calamoichthys*. It is therefore a question of considerable interest as to what is the relation of this fin to other known types, and how has it been formed. Upon this question two views have been held:—(1) The fin of *Polypterus* has been derived from a biserial archipterygium of the type of *Ceratodus* by the shortening of the axis and the shifting of the proximal radials up the axis to form the meta- and propterygia. This view has been mainly held by

Klaatsch [1] and Gegenbaur [2], though Gegenbaur appears now [3] to derive it directly from forms with a very short axis. (2) The fin of *Polypterus* has been derived from a uniserial fin of the type of *Heptanchus* or, perhaps better, *Chlamydoselache* by the shortening of the metapterygial border and the fusion of the bases of the radials to form the expanded mesopterygium.

Now the development of the fin might be expected to throw some light on this question, and in the 30 mm. larva this is what we find :—The general shape of the fin is quite different from that of the adult. The shape of the fin-blade is triangular, the metapterygial border forming with the distal border an acute angle, while the propterygial border forms with the distal border an obtuse angle (text-fig. 3. 2).

The cartilaginous skeleton of the pectoral fin differs in many important points from the skeleton of the fin of the adult *Polypterus*. The propterygium extending along the preaxial border of the fin is stout but short, being scarcely more than one-third the length of the metapterygium extending along the postaxial border, and being situated almost at right angles to the latter (Pl. XXXIII. fig. 8, *Pro.*). The angle between these two rods is filled by a flattened blade of cartilage, which is, however, slightly thickened where it is in contact with the metapterygium (Pl. XXXIII. fig. 8, *Mes.*). Distally this flat blade or mesopterygium is split in a fan-like manner to form the cartilaginous bases for the radials. The distal ends of these re-unite to form a continuous border of cartilage. The mesopterygial blade is irregularly punctured for the passage of blood-vessels (Pl. XXXIII. fig. 8, *b.v.f.*). On the free edge of the metapterygium, at its distal end, is a slight flange of cartilage, seemingly forming a rudimentary continuation round the distal end of the radial cartilages.

In fact the pectoral fin of the larva is not strictly a crossopterygium, but is a uniserial fin which can be directly compared with that of the Selachii.

The Pelvic Fin.—The cartilaginous skeleton of the very small pelvic fin consists of a rod of cartilage unsegmented and slightly curved, approximating its fellow at the anterior and posterior ends, but nowhere uniting with the latter (Pl. XXXIII. fig. 9, *Bas.*). The anterior extremities taper slightly and diverge, there being no indication of a distinct pelvic portion. Posteriorly these rods expand outwards and, as they penetrate the body-wall, each becomes split into four or five finger-like rods, some of which may re-unite distally. These form the cartilaginous bases of the radials (Pl. XXXIII. fig. 9, *r.*).

The development of the pelvic fin throws but little light on the morphology of the fins of *Polypterus*, but seems to confirm to some extent the view here taken from the development of the pectoral fin, that they have been derived from a uniserial type by shortening of the postaxial border, rather than from a biserial type by shortening of the median axis.

[1] Festschr. von C. Gegenbaur, part i. p. 261 (1896).

[2] Jen. Zeit. vii. 1873.

[3] Morph. Jahrb. xxii. p. 119.

IV.—Urinogenital Organs.

The excretory system of this larva is of especial interest, for here we find that a regular metamorphosis is taking place. The larval pronephros, though still functional, shows signs of degenerating, while the mesonephros is still fairly simple in its arrangement, and in some respects is still in a larval condition.

The pronephros consists of a rather small glomus almost filling the pronephric chamber which lies close by the aorta (Pl. XXXIV. fig. 9, *Gl.*); from this a narrow tube embedded in lymphoid tissue, the pronephric duct, passes outwards dorsal to the posterior cardinal vein and towards the body-wall (Pl. XXXIV. fig. 9, *pn.d.*); on passing between the dorsal and ventral lateral muscles it suddenly dilates, turns headwards, loops round the brachial nerve, and, in a mass of lymphoid tissue lying in the angle between the anterior ends of the dorso-lateral and ventro-lateral muscles and the skin, becomes greatly convoluted. In the successive convolutions the duct becomes narrower and narrower, occasionally becoming dilated and then suddenly narrower again; finally there leaves the convoluted mass a very fine duct (Pl. XXXIV. fig. 9, *s.d.*), and this, running along the outer side of the posterior cardinal vein, passes backwards and inwards until it comes to lie just over the peritoneum. Two segments behind the glomus of the head-kidney it gives off the first kidney-tubule, and thence passes straight to the hind end of the body-cavity as the segmental duct, ever increasing in size until it meets its fellow to form the urinary sinus (text-fig. 4, *u.s.*).

The smallness of the pronephric chamber and the dilatation of the convoluted portion of the pronephric duct must be regarded as signs of degeneration. In fact the connection between the pronephros and the mesonephros could not be traced on the left side, while on the right side it was done with the utmost difficulty. The glomus itself on the left side was very small, and the anterior end of the coiled pronepric duct could not be traced all the way to it.

On the right side there appeared to be traces of a peritoneal funnel leading to the pronephric chamber (Pl. XXXIV. fig. 9, *P.f.*); but with the thick sections into which I had cut this region (10 μ) I was unable to satisfy myself that it actually opened into this chamber.

In specimens 9 cm. in length all trace of the pronephros had disappeared, there remaining in its place a small mass of lymphoid tissue.

When we compare the pronephros of *Polypterus* with that of the Ganoids and Teleosteans which have been described, there can be no hesitation in saying that it resembles most closely the pronephros of *Amia* described by Jungersen[1], where there is one pronephric chamber, one peritoneal funnel, and one opening of the pronephric duct into the pronephric chamber. To draw a close comparison between

[1] Zool. Anz. 1894, p. 246.

Text-fig. 4.

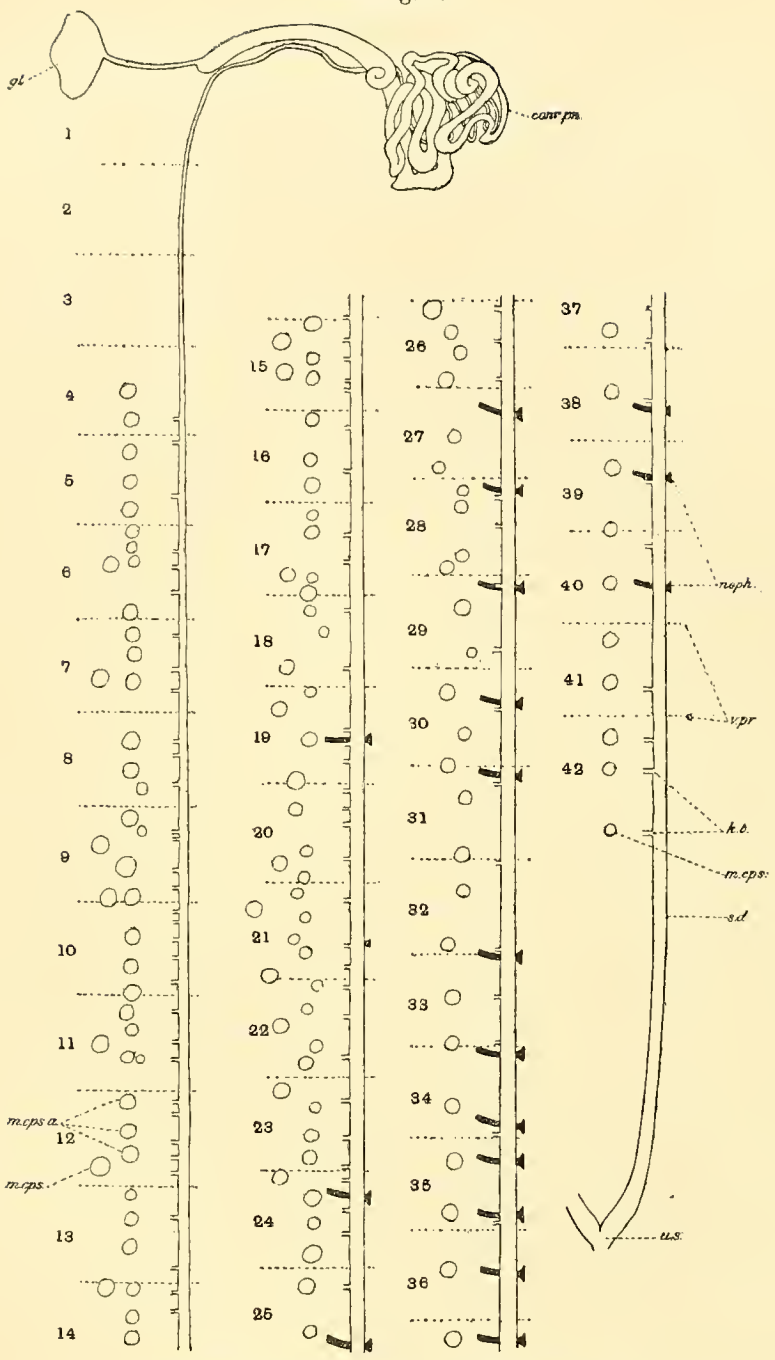


Diagram of kidney-system of larval *Polypterus*.

Projection from transverse sections of entire pronephros and mesonephros of the right side of the larva of the female *Polypterus*, × 60. The pronephros is a dorsal view of the same reconstruction as that figured in Pl. XXXIV. fig. 9.

gl. Glomus of pronephros.
conv.pn. Convoluted pronephric duct.
neph. Nephrostome.
v.pr. Position of ventral process marking the metameres.
k.t. Kidney-tubule.
m.cps. Glomerulus.
m.cps.a. Accessory glomeruli formed between the original glomeruli and the segmental duct.
s.d. Segmental duct.
u.s. Urinary sinus.

the pronephros of *Amia* and that of *Polypterus* is not possible, seeing that the stage I have described is undoubtedly only the last stage in the history of the pronephros.

Acipenser[1] has a very long pronephric chamber, with at first six, later four, funnels leading from the pronephric chamber.

Lepidosteus, according to Beard[2], has also at first a long chamber with three funnels, later a shorter one with two, and finally, according to Balfour[3] and Parker, only one funnel leads from the pronephric chamber.

It is of course conceivable that at an earlier stage *Polypterus* has more than one funnel leading from the pronephric chamber; but I think that this is not probable, seeing how widely is the glomus separated from the convoluted portion of the duct.

Lebedinsky[4] has described the pronephros of *Calamoichthys* as mingled with the anterior tubules of the mesonephros, somewhat as Semon describes the pronephros in *Ichthyophis*[5]. Seeing, however, that his "larvæ" measured 12 cm. and 15 cm. respectively, I think it would be surprising if in these young *Calamoichthys* there should remain traces of a pronephros which in *Polypterus* is already degenerating at 3 cm., and has completely disappeared at 9 cm. It is still more surprising that the larval head-kidneys of two creatures so closely allied as *Polypterus* and *Calamoichthys* bear no resemblance one to another. But it is not clear to me by what means the author of this account has distinguished between the tubules, "outer and inner funnels," &c. of the pronephros from those of the mesonephros. I am bound to conclude therefore that what Lebedinsky has described as "Vorniere" in *Calamoichthys* are some of the anterior tubules of the mesonephros, possibly accessory undeveloped ones, and that the pronephros ("Vorniere") has already disappeared.

At this stage the mesonephric tubules are already becoming complicated in the fore part of the body. There are from two to five glomeruli to each body-segment, and about the same number of tubules opening into the segmental duct (text-fig. 4). The accessory glomeruli and tubules arise close to the segmental duct, while the older formed ones become displaced and are found nearer the dorsal aorta towards the middle line (text-fig. 4, *m.cps.*). In the hinder half of the mesonephros the glomeruli become fewer and fewer, and the arrangement of the tubules simpler, while to each body-segment there is now found one glomerulus and one tubule opening into the segmental duct (text-fig. 4, *k.t.*). Throughout this portion of the body there is found lying immediately to the outer side of the genital ridge (ovary) and ventral to the segmental duct a strip of thickened peritoneal epithelium (Pl. XXXV. figs. 1, 2, 3, 4, 5, 6, 7, 8, *ov.d.*); this will eventually form the dorsal wall of the oviduct. *From the twenty-fourth to the fortieth segment there is found opening upon this thickened ridge in each segment a nephrostome communicating with the glomerulus* (Pl. XXXV. figs. 3, 4, *neph.*, & text-fig. 4, p. 331).

[1] Jungersen, Zool. Anz. 1893, pp. 464, 469.

[2] Anat. Anz. Bd. x. p. 94.

[3] *Loc. cit.*

[4] Jen. Zeitschr. 1891.

[5] Arch. mikr. Anat. xliv. p. 216.

Section I. (Pl. XXXV. fig. 1) is taken through the twenty-fourth segment, and shows the thickened strip of peritoneum in section lying to the outer side of the mesentery of the genital ridge (ovary) and the more complicated arrangement of tubules.

Section II. (Pl. XXXV. fig. 2) is taken through the twenty-ninth segment, and shows the thickened ridge (*ov.d.*) in section lying to the outer side of a small projection which here represents the genital ridge (*g.r.*). It also shows the accessory tubules on either side and the accessory glomerulus of the right side (*k.t.a.*, *m.cps.a.*). The arrangement of the older tubules is here less complicated.

Section III. (Pl. XXXV. fig. 3) is through the thirtieth segment, and shows on the left side a nephrostome opening upon the thickened ridge and communicating with the glomerulus (*neph.*, *m.cps.*). On the right side accessory tubules are shown (*k.t.a.*).

Section IV. (Pl. XXXV. fig. 4) is through the thirty-fourth segment; on the left side the edge of a nephrostome and also of a glomerulus is cut through (*neph.*, *m.cps.*), while on the right side is shown a single large glomerulus from which a kidney-tubule leads (*m.cps.*).

Section V. (Pl. XXXV. fig. 5) passes through the thirty-seventh segment, and shows the openings of two kidney-tubules into the right and left segmental duct (*k.t.*). The thickened ridge still persists, though the genital ridge does not extend so far back.

Section VI. (Pl. XXXV. fig. 6) is very near the hind end of the body-cavity behind the last kidney-tubules. The thickened ridge of peritoneum is still seen lying under the segmental duct (*ov.d.*, *s.d.*).

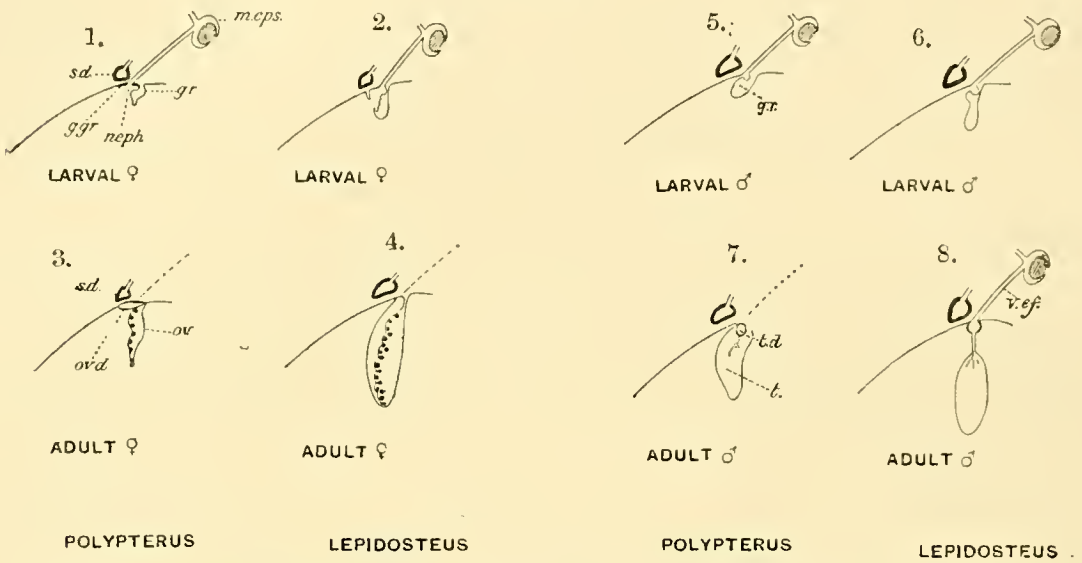
Section VII. (Pl. XXXV. fig. 7) is right at the end of the body-cavity; the segmental ducts are now turning ventralwards and approaching each other (*s.d.*), while the thickened ridge still lies just ventral to them (*ov.d.*)

Section VIII. (Pl. XXXV. fig. 8) passes just in front of the vent, behind the point of union of the segmental ducts. The body-cavity is seen here to be prolonged backwards in two portions on either side divided by a septum (*b.c.*); in the upper portions is still seen the thickened ridge of peritoneum (*ov.d.*). This upper portion is the commencement of the folding-off of the oviduct from the body-cavity by the forward growth of the septum, and it is at the point *x* that the oviducts eventually open into the urinogenital sinus. The lower portion of the body-cavity ends posteriorly at the point where the abdominal pores later break through (*a.p.*).

The further stages in the folding-off of the oviducts from the body-cavity I have been unable to observe, as in my next stage (9 cm.) the formation of the oviducts is already complete, though their posterior ends still end blindly in the wall of the urinary sinus. It is hardly possible to doubt, however, that the thickened ridge which we have traced through the posterior portion of the body-cavity forms eventually the dorsal wall of the oviduct. That is to say, we have, in the *Polypterus* larva, a row of nephrostomes opening into that portion of the body-cavity which will eventually become the genital duct.

In *Lepidosteus*, Balfour and Parker [1] found that the hollow ovary was formed by the ventral edge of the ovary growing round and fusing with the peritoneum, thus including a portion of the body-cavity. Into this cavity in the larval *Lepidosteus* they found nephrostomes opening; but Balfour says that he could not observe how the hind ends of the oviducts were formed, but admitted that if there should be found nephrostomes opening into this portion of the duct, it would prove that the oviducts of *Lepidosteus* are not true Müllerian ducts. Now this is precisely what we have in *Polypterus*. Jungersen [2] has shown that the ovary of many Teleosteans is formed by the inclusion

Text-fig. 5.



Series of diagrams illustrating the suggested homologies of the genital ducts and vasa efferentia in *Polypterus* and *Lepidosteus*.

neph., nephrostome of tubule passing to glomerulus; *m.cps.*, glomerulus; *g.gr.*, thickened strip of peritoneum or genital groove; *g.r.*, genital ridge; *s.d.*, segmental duct; *t.d.*, testis duct; *t.*, testis; *ov.*, ovary: *v.ef.*, vas efferens; *ov.d.*, oviduct.

The dotted line in 3, 4, and 7 indicates that the nephrostomes no longer persist. 5 and 6 indicate a condition believed to exist, but not yet proved.

of a portion of the body-cavity much as Balfour and Parker described the process in *Lepidosteus*, but, so far as I am aware, no one has found nephrostomes opening into the ducts of the ovary. It seems fairly certain, then, that in the female *Polypterus* the genital duct is not a Müllerian duct, that is, is not developed from the segmental duct.

In a previous paper [3] I described the genital duct in the male *Polypterus*, and gave reasons for regarding the genital ducts in the male and female as homologous structures, showing that in young specimens 9 cm. in length the hinder ends of the ducts in the

[1] *Loc. cit.* [2] Arb. Inst. Würzburg, Bd. ix. 1889.

[3] Trans. Zool. Soc. Lond. vol. xv. p. 323.

two series had a very similar appearance, but I was unable to show their actual origin. I have now indicated the origin of the genital duct in the female.

On re-examining my sections of the young male 9 cm. in length, I find an indication that the posterior part of the genital duct is formed in the same way, namely, by a folding-off of a groove in the cœlomic wall on the outer side of the genital ridge (Pl. XXXV. figs. 9, 10, *g.d.*).

Now this is precisely the region where in the female I have found the nephrostomes opening, and I can but suppose that the larval male possesses them too in early life. That is to say, in all probability, in the larva of the male *Polypterus* there will be found nephrostomes opening into that portion of the cœlom which becomes folded off to form the male genital duct. If, then, nephrostomes were retained in the adult, we should have formed a series of tubules connecting the genital duct with the glomeruli of the kidney; and if the genital duct ceased to perforate the wall of the urinary sinus the genital products could find their way out through the kidney, and the nephrostomes would be converted into vasa efferentia, similar to those of *Lepidosteus* and other Ganoidei, of Elasmobranchii, Dipnoi, Amphibia, and Amniota.

I suggest, then, that since I have previously given reasons for supposing that the genital ducts in the male and female *Polypterus* are homologous, the discovery of these nephrostomes opening into the female duct precludes the possibility of their being homologous with Müllerian ducts, but indicates a possible homology with the longitudinal canal of the testicular network of those forms in which such a network occurs, and the possible origin of the vasa efferentia, leading thence to the kidney, from nephrostomes.

Upon this view the genital ducts of *Polypterus*, Ganoidei, and Teleostei have arisen from a condition similar to that of the Cyclostomata, where the generative products are shed into the cœlom and pass into the ureter through genital pores. In *Polypterus* similar genital pores opening into the ureter upon a papilla are very early formed in male and female. From this condition, by the formation of first a groove, then a canal opening into the body-cavity anteriorly, and finally a canal continuous with the genital gland, the genital products were conducted outwards. Into this canal there opened a number of nephrostomes, which in the male of all forms except *Polypterus* and the Teleosteans took up the spermatozoa and became the vasa efferentia (text-fig. 5).

It is true that there is very little ontogenetic evidence of this mode of the formation of the vasa efferentia. But the fact that in all forms where nephrostomes leading from the cœlom to the kidney persist they are absent in the region of the testicular network, would fit in with the view that the nephrostomes in this region have been used to form the vasa efferentia.

Jungersen in his work on the genital ducts of Teleosteans[1] cites evidence brought

[1] *Loc. cit.*

forward by Siebold and by Brock, that in certain Teleosteans in which the testes are hollow, the cavity of the testis, and therefore probably also of the testis-duct, is formed by a folding-off of a portion of the cœlom.

Jungersen came to the conclusion that in all Vertebrata except Elasmobranchs the oviducts were homologous and formed by a folding-off of a groove in the cœlomic wall. If this conclusion is correct, then there is a difficulty in the way of the view I have put forward which it is not easy to overcome. In many forms which possess a testicular network there is also found, in the male, a more or less rudimentary female genital duct usually called a Müllerian duct. It seems unlikely, then, to say the least of it, that, in these forms, the longitudinal canal of the network in the male and the genital duct of the female can be homologous, for these structures occur side by side in the males.

If the ducts of Ganoidei and Teleostei really are homologous in the male and female, while in the other Gnathostomata they are not homologous, then either the female duct or the male duct cannot be homologous throughout the Gnathostomata.

It can, I think, hardly be doubted that the male and female ducts in Teleostei are homologous. I have before given reasons for thinking that they are so in *Polypterus*. It remains, then, to decide whether it is more likely that the male duct in *Polypterus* is homologous with the longitudinal canal of *Lepidosteus* and so with that of other forms in which a testicular network occurs, or that the female duct in Ganoidei, Crossopterygii, and Teleostei is homologous with the female duct of other Gnathostomata, as held by Jungersen.

The male duct of *Polypterus* lies in exactly the same position as the blind longitudinal canal of *Lepidosteus*, and it is difficult to avoid the conclusion that these ducts are homologous with one another, and again that this canal in *Lepidosteus* is the longitudinal canal of the testicular network of other forms.

Jungersen [1] admits this comparison, but derives the male duct of *Polypterus* and Teleostei from the fusion of a testicular network with the loss of its connection with the kidney, which he, with Semon [2] and Kerr [3] and many other authors, regards as the primitive condition. But Jungersen [4] also holds that the female ducts are homologous throughout the Gnathostomata. The presence of the rudimentary Müllerian duct in many forms with a testicular network makes it impossible on this view to regard the ducts of male and female in any vertebrate as homologous structures, as they appear to be in Teleostei.

Supposing, however, that the female ducts in *Polypterus*, Ganoidei, and Teleostei are not homologous with those of Elasmobranchii and Amniota, as their position in the hind end of the body-cavity, and the presence in *Polypterus* and *Lepidosteus* of

[1] Zool. Anz. xxiii. Bd. No. 617.
[2] Jen. Zeitschr. 1891.
[3] Proc. Zool. Soc. 1901, vol. ii. p. 493.
[4] Arb. Inst. Würzburg, Bd. ix. 1889.

nephrostomes opening into them, makes very probable, then we may regard the male and female ducts of Cyclostomata, Crossopterygii, Ganoidei, and Teleostei as homologous, and the female ducts of other Gnathostomata as independent structures, *i. e.* Müllerian ducts. It is now known that these Müllerian ducts arise as a splitting off from the Archinephric duct only in Elasmobranchs, but this difference in the mode of origin of the oviducts is not considered by many authors to constitute a proof that they are not homologous. The peculiarity of the oviducts of these groups (Elasmobranchii, Dipnoi, Amphibia, and Amniota) in tending to appear in the males as more or less rudimentary structures, seems to me to be a strong argument in favour of their being homologous in these groups; and it is very noticeable that these rudiments are usually, if not invariably, absent in the Crossopterygii, Ganoidei, and Teleostei, those groups, namely, in which the oviduct in the female appears not to be homologous with the Müllerian ducts but rather with genital ducts of the male.

Summary of the Structure and Development of the Urinogenital Organs.

The pronephros of *Polypterus* is beginning to degenerate in the larva 30 mm. in length. At this stage it consists of a small pronephric chamber containing the glomus and of a duct leading from the chamber to pass to and become the duct of the mesonephros, and consisting of three portions—a very narrow portion leading outwards, a dilated and much convoluted portion lying close under the skin, and a very narrow portion leading inwards and backwards to become the segmental duct of the mesonephros.

The pronephros of *Polypterus* resembles very much that of *Amia*.

The mesonephros anteriorly is at this stage becoming complicated. Posteriorly it has still a segmental arrangement, each segment being provided with one Malpighian corpuscle with its tubule leading to the segmental duct and its peritoneal funnel. The peritoneal funnels open upon the rudiment of the oviduct, which is not yet folded off from the cœlom. The genital pores do not yet penetrate the walls of the urinary sinus.

From examination of somewhat older specimens, the male and female ducts appear to arise in a somewhat similar manner, and it is regarded as probable that in the young male larva the peritoneal funnels open upon the rudiment of the male duct. It is suggested that these peritoneal funnels, if they persisted, would then answer to the vasa efferentia passing from the longitudinal canal to the Malpighian corpuscles of *Lepidosteus*.

The male and female ducts of Crossopterygii and Teleostei are regarded as homologous structures, which in the males of other Gnathostomata have been gradually absorbed in the testicular network, and in the females of other Gnathostomata except the Ganoidei are replaced by Müllerian ducts.

Whatever be the true interpretation of the genital ducts in the Ichthyopsida, the Crossopterygii, Teleostei, and Ganoidei are closely united in this respect, the latter group appearing to stand in closer relationship to the rest of the Gnathostomata than the former groups.

V.—Conclusion.

We have seen, then, that in its development *Polypterus* shows affinities in various directions. The development of the pectoral fin and of the cranium and visceral arches has some resemblance to that of the Elasmobranchii, while of course the spiral valve, the conus and optic chiasma in the adult are other structures common to the two groups. The development of the vertebral column is not very dissimilar to that of the Teleostei, though in the possession of lateral cartilaginous processes in addition to the neural and ventral processes of the Dipnoi, Ganoidei, and Teleostei, *Polypterus* presents a very generalized condition; while there can be no doubt that from the standpoint of urinogenital organs both the larval and adult *Polypterus* are as closely connected with the Teleostei as even *Amia* itself. It has, however, been admitted by the most competent palæontologists that the structure of the dermal bones of the head and of the shoulder-girdle of *Polypterus* is so like that of certain Stegocephali, that it must be regarded as more than a mere resemblance, while there are many points in the development of the skeleton that distinctly approach the condition of the Amphibia. The only possible interpretation of these facts appears to me to be that the living Crossopterygians form a central group among recent forms having some characters in common with most of the great groups. Seeing that it is thus a generalized form and is not very different from the ancient Devonian Crossopterygii, it seems to me not improbable that the particulars of structure in which it resembles the admittedly recent Teleostei are in both groups of a primitive nature. I do not pretend that upon this point I feel very certain, but I think I have put forward some evidence in favour of the view I have taken.

It is with reluctance that I publish a piece of work the material for which consisted of a single specimen; but as there seemed to be no prospect in the immediate future of an abundant supply of the early stages in the development of *Polypterus* being obtained, and as upon examination I found that there were points of considerable interest in this small larva, it seemed only right that they should be known. I trust, however, that when more material comes to hand it will be found that what has been seen in this larva has been accurately described.

PLATE XXXIII.

PLATE XXXIII.

Fig. 1. A side view of a reconstruction from transverse sections, 10 μ in thickness, of the right half of the primordial cranium and visceral arches of the larval *Polypterus*. The great afferent and efferent blood-vessels to the external gill are also shown. The last section of the reconstruction cuts off the exoccipital region, the third and fourth branchial arches, and the afferent and efferent vessels to the external gill.

Fig. 2. A posterior view of the same, reconstructed. The cut surfaces of the cartilage where the reconstruction ends posteriorly are dotted. The anterior region of this reconstruction has also been cut off just behind the nasal capsules.

Fig. 3. Anterior aspect of the same. The cut surfaces are dotted. The portion reconstructed is the same as for fig. 2.

Fig. 4. Reconstruction of the left side of the occipital region and anterior end of the vertebral column, showing that the exoccipital cartilage has still the form of a neural arch, though already fused to some extent above and below with the cranium. The lateral and ventral processes are seen to be very long in this region. The parachordal cartilages are shown to send a bridge of cartilage under the aorta.

Fig. 5. A dorsal view of a reconstruction of a portion of the mid-region of the vertebral column [1]. The dorsal spines have been cut off.

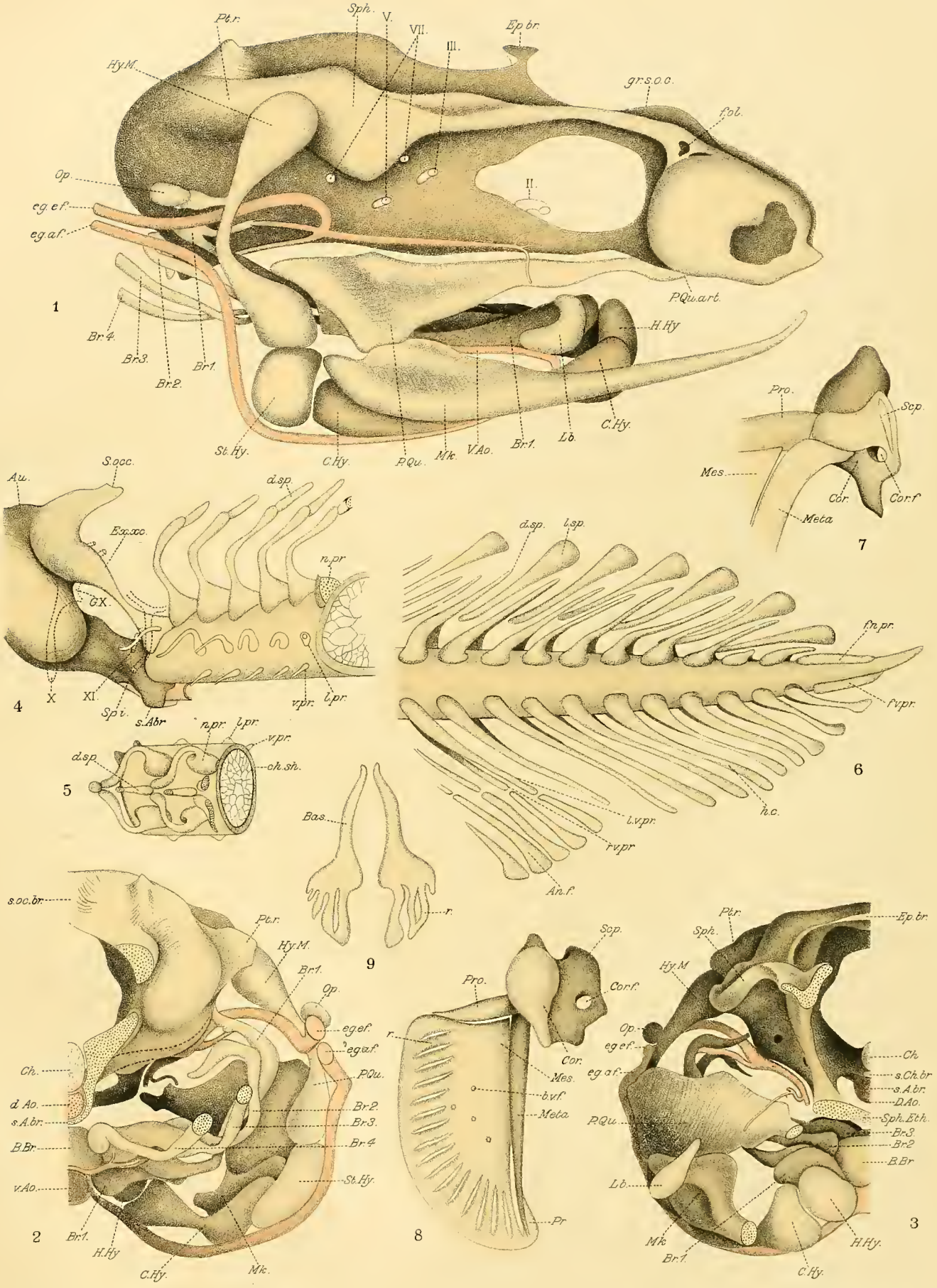
Fig. 6. Reconstruction of the caudal portion of the axial skeleton showing the form of the neural and ventral arches at this stage and the manner in which the anal fin is supported; also the very slight upward tendency of the termination of the notochord.

Fig. 7. Reconstruction of the cartilage of the left half of the shoulder-girdle, seen from behind.

Fig. 8. Reconstruction of the shoulder-girdle and left pectoral fin, seen from the front, showing the great length of the metapterygium as compared with that of the propterygium and the formation of the radials from one continuous plate of cartilage.

(Fig. 8 of this Plate is × 20; all the other figures are × 30.)

[1] The *anterior* end of this portion is to the *right*.



J.S.B.del.

E.Wilson lith. Cambridge.

STRUCTURE OF THE LARVAL POLYPTERUS.

PLATE XXXIV.

PLATE XXXIV.

Fig. 1. A section through the alisphenoid region of the head cutting the median vesicle, epiphysis, and cartilaginous bridge in the region of the epiphysis, also cutting the trabeculæ cranii, the sphenotic wings, and palato-quadrate bars. × 30.

Fig. 2. A section through the vertebral region of the axial skeleton in the anterior part of the body of the 30 mm. larva. Showing the neural, lateral, and ventral processes abutting on the notochord, also the outer portion of the cartilages of the lateral ribs. × 30.

Fig. 3. A section through the same region in a 9 cm. specimen, showing the encrusting bony deposits forming the vertebræ with their large transverse process. The ventral processes no longer abut on the notochord. × 22.

Fig. 4. A similar section in the hind part of the body of a 9 cm. specimen, showing the cartilaginous ventral processes now forming the heads of the ventral ribs attached to the undersides of the extremities of the bony transverse processes. The ventro-lateral muscles likewise have retreated from contact with the notochord. × 22.

Fig. 5. A section through the vertebral region of the axial skeleton in the anterior part of the body of a 13 cm. specimen, showing the increased development of the bony vertebræ, the complete suppression of the cartilages of the axial skeleton, and the vertebrally constricted notochord. × 15.

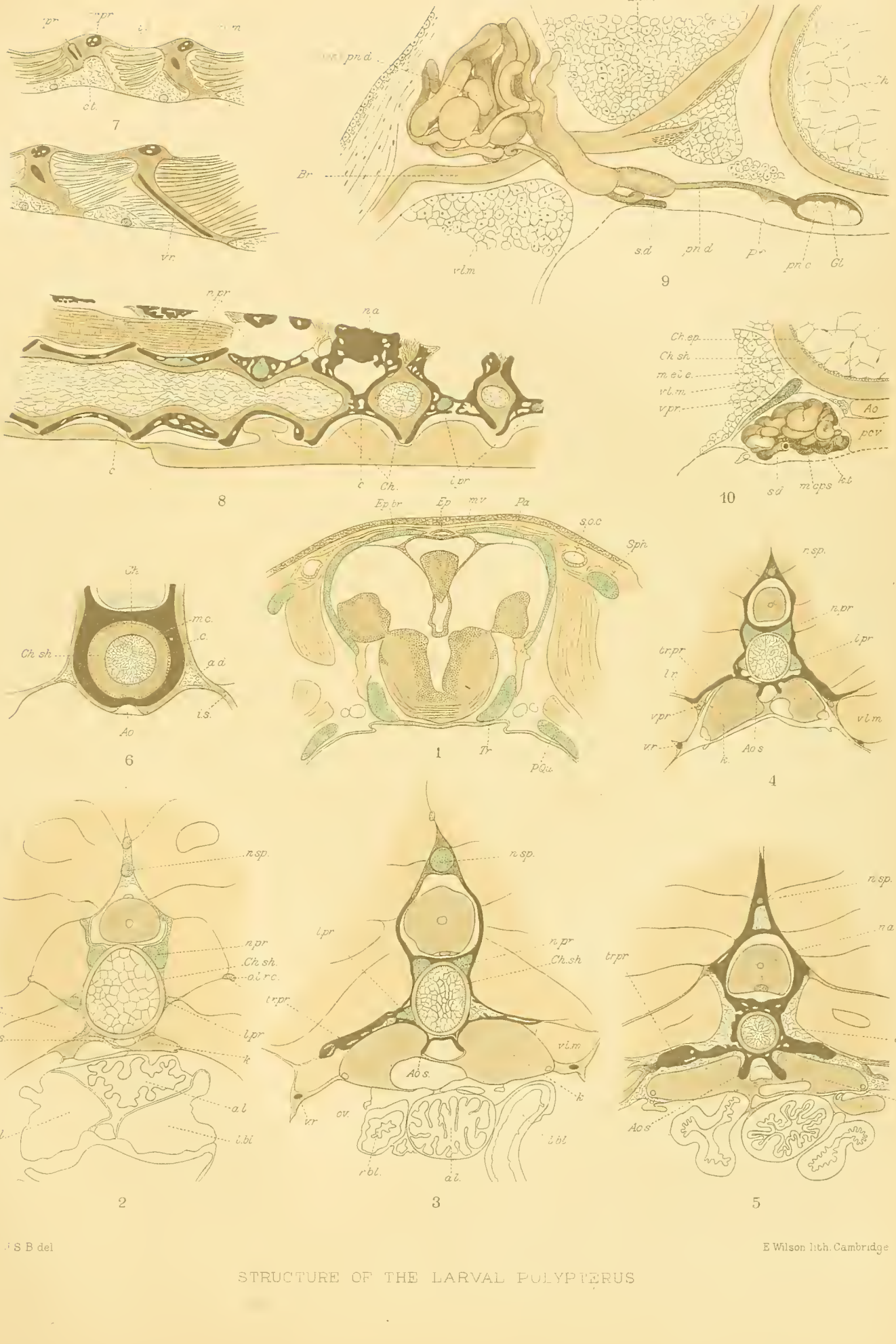
Fig. 6. A section through the intervertebral region of the same series as fig. 5, showing the intervertebral dilatation of the notochord, especially of its sheath, which is enclosed in a single layer of cartilage-like cells. × 15.

Fig. 7. A slightly oblique longitudinal section through the ventro-lateral muscles in a 9 cm. specimen, showing the head of the ventral rib to the left containing the cartilage of the ventral process and lying in front of the transverse process, and the continuation of the ventral ribs outwards and backwards towards the right. The figure has been put on the Plate in two portions. × 20.

Fig. 8. A section of the same series as fig. 7, but in the middle of the vertebral centra on the left, sloping ontwards through the sides of the vertebræ towards the right. Two cartilaginous neural processes are seen towards the middle of the figure embedded in the bony centra, further to the right the section passes through the bony neural arch, while on the right of the figure are seen two lateral cartilaginous processes. × 20.

Fig. 9. Is a reconstruction of the pronephros of the right side of the 30 mm. larva, and viewed from the headward side, with the glomus lying under the notochord and the coiled portion of the pronephric duct lying between the brachial nerve and the skin. The notochord, dorso-lateral muscles, and ventro-lateral muscles are seen only in section. × 70.

Fig. 10. Is a similar reconstruction of the most anterior mesonephric tubules of the right side, showing that they do not lie in the same region of the body as the coiled duct of the pronephros, but much nearer the middle line close under the notochord, and that they end anteriorly quite suddenly. × 70.



J S B del

E Wilson lith. Cambridge

STRUCTURE OF THE LARVAL POLYPIERUS

PLATE XXXV.

PLATE XXXV.

Fig. 1. A section through the mesonephros of the 24th body-segment, showing the thickened strip of peritoneum in section lying to the outer side of the mesentery of the genital ridge (ovary) and the more complicated arrangement of the tubules in the anterior region.

Fig. 2. A section through the 29th body-segment, showing the thickened ridge lying to the outer side of a small projection, which here represents the genital ridge. It also shows the accessory tubules on either side and the accessory glomerulus on the right side. The arrangement of the older tubules is here less complicated.

Fig. 3. A section through the 30th body-segment, showing on the left side a nephrostomic opening upon the thickened ridge and communicating with the glomerulus. On the right side accessory tubules are shown.

Fig. 4. A segment through the 34th body-segment; on the left side the edge of a nephrostome and also of a glomerulus is cut through, while on the right side is shown a single large glomerulus from which a kidney-tubule leads.

Fig. 5. A section through the 37th body-segment, showing the opening of two kidney-tubules into the right and left segmental duct. The thickened strip of peritoneum still persists, though the genital ridge does not extend so far back.

Fig. 6. A section passing near the hind end of the body-cavity behind the last kidney-tubules. The thickened strip of peritoneum is still seen lying under the segmental duct.

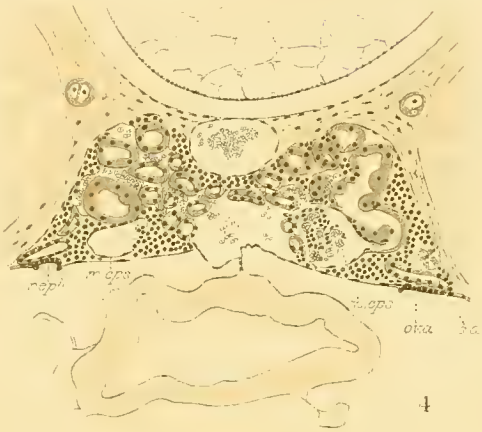
Fig. 7. A section passing through the very end of the body-cavity; the segmental ducts are now turning ventralwards and approaching one another, while the thickened strip lies just ventral to them.

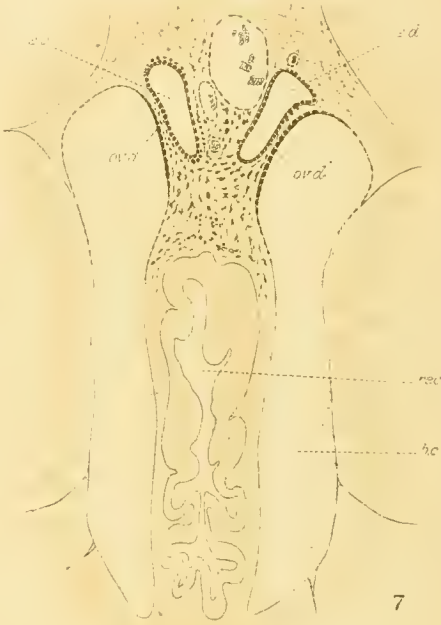
Fig. 8. A section passing just in front of the vent, behind the point of union of the segmental ducts. The body-cavity is seen here to be prolonged backwards in two portions on either side divided by a septum. The thickened strip of peritoneum is here seen on the inner side of the dorsal portion.

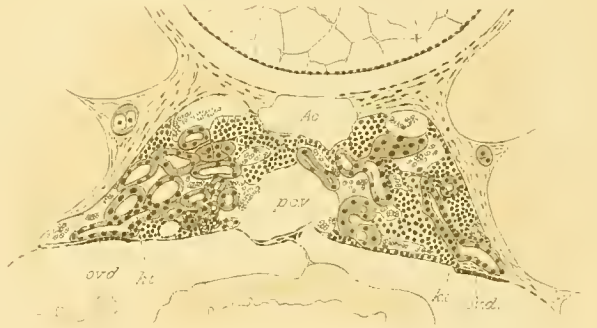
Fig. 9. A section through the posterior end of the kidneys of a 9 cm. male specimen, showing the genital duct still in connection with the peritoneal epithelium.

Fig. 10. A section of the same specimen further forwards, showing the large size of the genital duct at the base of the testis.

(Magnification 80.)







J S B.del

E Wilson lith Cambridge

STRUCTURE OF THE LARVAL [illegible]CYPTERUS

Lettering of the Figures.

ad. Adipose tissue.
al. Alimentary canal.
An.f. Anal fin.
Ao. Dorsal aorta.
Ao.s. Aortic supports.
a.p. Abdominal pore.
Au. Auditory capsule.
Bas. Basipterygium.
b.c. Body-cavity.
B.Br. Basibranchial cartilage.
Br. 1, 2, 3, 4. Branchial cartilages 1, 2, 3, 4.
Br.n. Brachial nerve.
b.v.f. Blood-vessel foramen.
c. Centrum.
Ch. Notochord.
Ch.ep. Chorda epithelium.
Ch.sh. Sheath of notochord.
C.Hy. Ceratohyal.
conv.pn.d. Convoluted pronephric duct.
Cor. Coracoid.
Cor.f. Coracoidal foramen.
d.Ao. Dorsal aorta.
d.l.m. Dorso-lateral muscles.
d.sp. Dorsal spines.
eg.af. Afferent artery to external gill.
eg.ef. Efferent artery to external gill.
Ep. Epiphysis.
Ep.br. Bridge of cartilage in region of epiphysis.
Ex.oc. Exoccipital cartilage.
f.n.pr. Fused neural processes.
f.ol. Foramen for olfactory branches of vth and viith nerves.
f.v.pr. Fused ventral processes.
G.x. Vagus ganglion.
g.d. Genital duct.
Gl. Glomus.
g.r. Genital ridge.
gr.s.o.c. Groove for the supraorbital canal.
h.c. Hæmal cartilage.
H.Hy. Hypohyal.
Hy.M. Hyomandibular.
i.s. Intermuscular septum.
k. Kidney.
k.t. Kidney-tubule.
k.t.a. Accessory kidney-tubule.
Lb. Labial cartilage.
l.bl. Left swim-bladder.
l.pr. Lateral process.
l.r. Lateral rib.
l.sp. Interspinous cartilages.
l.v.pr. Left ventral process.
m.cps. Glomerulus.
m.cps.a. Accessory glomerulus.
m.c. Cartilage-like cells of membrana elastica externa.
m.el.e. Membrana elastica externa.
Mes. Mesopterygium.
Meta. Metapterygium.
Mk. Mandibular cartilage.
m.v. Median vesicle of brain.
n.a. Neural arch.
neph. Nephrostome.
n.pr. Neural process.
n.sp. Neural spine.
o.l.r.c. Outer cartilages of the lateral ribs.
Op. Operculum.
ov. Ovary.
ov.d. Oviduct.
Pa. Palium.
p.c.v. Posterior cardinal vein.
P.f. Peritoneal funnel (traces of).
pn.c. Pronephric chamber.
pn.d. Pronephric duct.
Pr. Rudimentary continuation of radials.
Pro. Propterygium.
P.Qu. Palato-quadrate cartilage.
P.Qu.art. Palato-quadrate articulation.
Pt.r. Pterotic ridge.
r. Cartilaginous bases of radials.
r.bl. Right swim-bladder.
rect. Rectum.
r.v.pr. Right ventral process.

s.A.br. Subaortic bridge.
Scp. Scapula.
s.Ch.br. Subnotochordal bridge.
s.d. Segmental duct.
s.o.c. Supraorbital canal.
S.occ. Supraoccipital region.
s.oc.br. Supraoccipital bridge.
Sph. Sphenotic.
Sph.Eth. Cartilage of sphenethmoid region.
Sp.i. First spinal nerve.
st. Stomach.
St.Hy. Stylohyal.
T. Testis.
Tr. Trabeculæ cranii.
tr.pr. Transverse bony process.
u.s. Urinary sinus.
V.Ao. Ventral aorta.
v.l.m. Ventro-lateral muscles.
v.pr. Ventral process.
v.r. Ventral rib.
x. Point where oviduct will open into urinary sinus.
II., III., V., &c. Positions of exit of cranial nerves.

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

(continued).

	To Fellows. £	s.	d.	To the Public. £	s.	d.
VOLUME XIV. (1896–1898, containing 47 Plates) . Price	5	5	0	7	0	0
Part 1. (1896, containing 2 Plates) . . . . . „	0	6	0	0	8	0
„ 2. (1896, containing 6 Plates) . . . . . „	0	9	0	0	12	0
„ 3. (1897, containing 9 Plates) . . . . . „	0	15	9	1	1	0
„ 4. (1897, containing 10 Plates) . . . . . „	1	10	0	2	0	0
„ 5. (1898, containing 2 Plates) . . . . . „	0	6	0	0	8	0
„ 6. (1898, containing 7 Plates) . . . . . „	0	18	0	1	4	0
„ 7. (1898, containing 6 Plates) . . . . . „	0	11	3	0	15	0
„ 8. (1898, containing 5 Plates and Title and Index) „	0	9	0	0	12	0
VOLUME XV. (1898–1901, containing 52 Plates) . Price	5	15	6	7	14	0
Part 1. (1898, containing 8 Plates) . . . . . „	0	15	9	1	1	0
„ 2. (1899, containing 5 Plates) . . . . . „	0	9	0	0	12	0
„ 3. (1899, containing 4 Plates) . . . . . „	0	9	0	0	12	0
„ 4. (1899, containing 4 Plates) . . . . . „	0	9	0	0	12	0
„ 5. (1900, containing 24 Plates) . . . . . „	2	12	6	3	10	0
„ 6. (1901, containing 4 Plates) . . . . . „	0	11	3	0	15	0
„ 7. (1901, containing 3 Plates and Title and Index) „	0	9	0	0	12	0
VOLUME XVI.						
Part 1. (1901, containing 6 Plates) . . . . . Price	0	18	0	1	4	0
„ 2. (1901, containing 5 Plates) . . . . . „	0	11	3	0	15	0
„ 3. (1901, containing 9 Plates) . . . . . „	0	15	9	1	1	0
„ 4. (1902, containing 5 Plates) . . . . . „	0	9	0	0	12	0
„ 5. (1902, containing 4 Plates) . . . . . „	0	13	6	0	18	0
„ 6. (1902, containing 3 Plates) . . . . . „	0	15	9	1	1	0
„ 7. (1902, containing 3 Plates) . . . . . „	0	11	3	0	15	0

CONTENTS.

VIII. *On the Structure of the Larval* Polypterus. *By* J. S. Budgett, M.A., F.Z.S. (Plates XXXIII.–XXXV.) . . . . . page 315

THE PUBLICATIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

The scientific publications of the Zoological Society of London are of two kinds—"Proceedings," published in an octavo form, and "Transactions," in quarto.

According to the present arrangements, the "Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the "Proceedings" by the Committee of Publication. A large number of coloured plates and engravings are attached to each annual volume of the "Proceedings," to illustrate the new or otherwise remarkable species of animals described in them. Among such illustrations, figures of the new or rare species acquired in a living state for the Society's Gardens are often given.

The "Proceedings" for each year are issued in four parts, on the first of the months of June, August, October, and April, the part published in April completing the volume for the last half of the preceding year. Commencing from January 1901 they form two half-yearly volumes.

The "Transactions" contain such of the more important communications made to the scientific meetings of the Society as, on account of the nature of the plates required to illustrate them, are better adapted for publication in the quarto form. They are issued at irregular intervals.

Fellows and Corresponding Members, upon payment of a Subscription of £1 1*s*. before the day of the Anniversary Meeting in each year, are entitled to receive all the Society's Publications for the year. They are likewise entitled to purchase the Publications of the Society at 25 per cent. less than the price charged for them to the Public. A further reduction of 25 per cent. is made upon purchases of Publications issued prior to 1871, if they exceed the value of five pounds.

Fellows also have the privilege of subscribing to the Annual Volume of the 'Zoological Record' for a sum of £1 (which includes delivery in the United Kingdom *only*), but this privilege only holds good if the subscription is paid before the First of December in each year.

Such of these publications as are in stock may be obtained at the Society's Office (3 Hanover Square, W.), at Messrs. Longmans', the Society's publishers (Paternoster Row, E.C.), or through any bookseller.

October, 1902.

P. L. SCLATER,
Secretary.

590642

TRANSACTIONS

OF

THE ZOOLOGICAL SOCIETY OF LONDON.

VOL. XVI.—PART 8.

LONDON:

PRINTED FOR THE SOCIETY,

SOLD AT THEIR HOUSE IN HANOVER-SQUARE;

AND BY MESSRS. LONGMANS, GREEN, AND CO., PATERNOSTER-ROW.

May 1903.

Price 18*s*.

Smithsonian Institution, 187349 JUN 30 1903 National Museum.

Taylor and Francis, Printers.] [Red Lion Court, Fleet Street.

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

	To Fellows. £ s. d.	To the Public. £ s. d.
VOLUME I. (1833–1835, containing 59 Plates) . . Price	3 13 6	4 18 0*
VOLUME II. (1835–1841, containing 71 Plates) . . „	4 0 0	5 6 6*
VOLUME III. (1842–1849, containing 63 Plates) . . „	3 8 3	4 11 0*
VOLUME IV. (1851–1862, containing 77 Plates) . . „	6 2 0	8 2 6†
VOLUME V. (1862–1866, containing 67 Plates) . . „	5 4 3	6 19 0†
VOLUME VI. (1866–1869, containing 92 Plates) . . „	11 5 0	15 0 0†
VOLUME VII. (1869–1872, containing 73 Plates) . . „	10 4 0	13 12 0†
VOLUME VIII. (1872–1874, containing 82 Plates) . . „	9 8 3	12 11 0†
VOLUME IX. (1875–1877, containing 99 Plates) . . „	12 1 6	16 2 0†
VOLUME X. (1877–1879, containing 95 Plates) . . „	10 0 3	13 7 0†
GENERAL INDEX, Vols. I. to X. (1833–1879) . „	0 7 6	0 10 0
VOLUME XI. (1880–1885, containing 97 Plates) . . „	9 12 0	12 16 0
VOLUME XII. (1886–1890, containing 65 Plates) . . „	5 8 0	7 4 0
VOLUME XIII. (1891–1895, containing 62 Plates) . . „	6 8 3	8 11 0

* No copies of these volumes remain in stock.

† Only complete copies of these volumes are left in stock.

Continued on page 3 of Wrapper.

IX. *Ecdysis, as Morphological Evidence of the Original Tetradactyle Feathering of the Bird's Fore-limb, based especially on the Perennial Moult in* Gymnorhina tibicen.

By Edward Degen, *F.Z.S.*

Received October 16, 1901; read February 4, 1902.

[Plates XXXVI.–XXXVIII.]

Contents.

	Page
I. Introductory	347
II. Historical	348
III. Method of Research	351
IV. Explanatory Remarks on the Diagrams on Plates, Tables, and Charts	354
V. Definition of "Moult"	355
A. On "Adventitious Plumage"	355
B. On the "Feathering of the Fledgling"	363
C. On "Perennial Feathering"	365
VI. "Orders of the Moult" in *Gymnorhina tibicen*	367
A. Flight-feathers or Pennæ alares = Remiges primores plus Remiges cubitales (Sundevall)	367
B. Remarks on the Period of Growth and the Development of the Remiges	371
C. The Bastard Wing. Alula or Ala spuria = Plumæ pollices	371
D. Extract from and Remarks on the Table of Percentages for the Deficiency in the Power of Flight	375
E. The Wing-coverts or Tectrices	376
VII. Summary of the Order in the Perennial Moult of the Wing-feathers	390
VIII. The Contour Feather-tracts or Pterylæ	395
IX. Conclusions	400
X. Bibliography	410
XI. Explanation of the Plates	412

I.—Introductory.

The main object of this paper is to give additional evidence in support of the theory of the derivation of the feathering of the bird's wing.

When I was engaged on the subject of Diastataxy (Aquinto-cubitalism), the peculiar conditions of the flight-feathers during the moult seemed to indicate that, by a fuller study of the perennial moult, the facts concerning the observations of the feathers of the bird's wing might be considerably elucidated.

In order, then, to form a solid foundation for the purely morphogenetic development of the feathers, it was necessary to ascertain the mode by which the perennial moult of the individuals of a species of bird is made up, from the earliest to the last stages of renewal; and, further, to what extent each feather participates in this annual

process during the period of complete feather-change. This has been methodically treated and fully explained in the present paper.

By a "feather-change" there can be meant one thing only, namely, the actual renewal of all the feathers.

Physical changes, arising from external agencies, such as colour-changes, or the abrasion of the wing-coverts and contour-feathers of the body, with their attendant effects upon the pattern of the plumage, do not enter into the scope of this work. Neither do partial changes, such as spring-plumages and the various forms of nuptial garbs, of a sexual nature; nor do the phenomena of "Albinism" and "Melanism," all these being either of a secondary origin, or, as in the latter case, of an ætiological nature.

II.—Historical.

With regard to the literature, it may be well to review in a general way those papers which deal with the morphological history of the feathers. For a more exhaustive account of the history of the "moult," I refer the reader to the excellent article of Dr. Allen (1), who has considered previous authors chronologically, and at the same time has himself contributed to the physiology of the subject.

By far the most important addition to the subject of "moult" was that made by Blyth (4) in 1837, who, amongst other observations relative to colour-changes, makes remarks on the plumage of birds which are of great value. Among many excellent attributes characterizing his work, is that of a comparatively far advanced pterylographic knowledge before the time of appearance of the classic treatise of Nitzsch's 'Pterylography,' edited by Burmeister, and first published in 1840 (Translation, 37)[1].

Blyth's work is replete with information, based principally on the "Mallard" and the "Widgeon"; but though he bestowed much care on the partial and perennial moult of the primaries and the tail-feathers, he treated but scantily the wing-coverts. To this author's paper I have made frequent reference in the course of my own research.

Schlegel's famous "Address" (40) gave a new impetus to the subject of ecdysis. I shall have to allude more particularly in the course of my own work to the various

[1] Yarrell's endeavour to adduce evidence in favour of his view, "*that the feather itself becomes altered*"[a]—though in the course of his arguments he admits "that it is certainly difficult to understand how this is so constantly effected in the web of the feather, *where no vascularity can be shown to exist*[a], even when the part is growing" (*cf.* Allen, *l. c.*),—is shared also by Blyth to a great extent. Burmeister's observations and researches into the histological structure of the feather (see Nitzsch, *l. c.*), and also Holland (29), should, however, finally dispel any doubts still existing on the point of a revitalization of the feather.

[a] These *italics* are mine.

statements made by this author under the different chapters. Allen has criticized it in a general way.

Amongst the principal dissentients from the laws formulated by Schlegel respecting the season, manner, degrees, and methods of moult and alleged changes of colour without moult, should be mentioned, as the foremost, Homeyer, who in 'Rhea,' ii. 1846, p. 157, published some remarks; he also replied to Schlegel in a communication to 'Naumannia' (1853), and further by numerous comments on this subject (see Bibliography, 30, 30 *a*, 31).

To the most prolific writers of that period who subjected the seasonal and other changes to a fuller scrutiny, unquestionably belongs Brehm (6, 7, 8, 9, & 10) by reason of a large amount of material gathered for this purpose by his son Alfred. However, apart from the profusion of *a priori* argument and some other additional information, his inquiries had to a great extent the object of refuting the "thesis" laid down by Schlegel, and also similar views held by Martin (32, 33).

Important contributions to the knowledge of the chemico-physical changes in the feather-structure itself were those of Altum (2), Meves (34), and Bogdanow. Meanwhile the question gave rise to a number of minor contributions, consisting of critical remarks or casual observations on the subject, such as those of Gloger (24, 25, 26), Hesler (28), Böck (5), Dwight (18), v. Müller (36), Gätke (22), Cabanis, and many others.

Until the appearance of the translation from the Swedish of Sundevall's work (43), a great deal of confusion existed in regard to a scientific knowledge of the topography of the feathering in birds. Sundevall has done much to remedy this deficiency, and confined his researches largely to this character, though principally to the serial values, of the feathers on the wing.

It is from this point that the researches conducted into the derivation of the plumage began in earnest, as Nitzsch's 'Pterylography,' which appeared in 1840, seems to have been little known or appreciated by his own countrymen, and it was not until the able translation into English, published in 1867 by Dr. P. L. Sclater for the Ray Society, was available that its worth became generally recognized. And in reading Nitzsch, it is not a little remarkable to find that the portion dealing with the covert-feathers on the wing should have received so little attention. Nevertheless, it is to the last-named authors, Sundevall and Nitzsch (37), that we are primarily indebted for a beginning of the study of the morphological question concerning the feathering of the wings of birds.

After this, with the exception of two short papers in 1856 by Dr. Weinland—one in Journ. f. Ornith. iv. pp. 125–129, and the other in Proc. Boston Soc. Nat. Hist. iv. (1856–59) pp. 34–37,—a period of calm set in, which was broken only by the important work published in 1866 by Dr. Fatio (19), who had meautime conducted a series of investigations into the changes of the plumage, both chemico-physical and physiological. To this memoir I have been frequently indebted.

After Fatio's publication, the subject again lapsed, when it was reopened in 1877 with a short contribution by Gerbe (23). To this author we are indebted for the first allusions made to the genetic relations of the flight-feathers and their coverts. Gerbe refers the student, at the beginning of his paper (which seems to have been merely intended as a preliminary article), to some subsequent and more comprehensive account of this subject. This appears never to have been published. This author's researches do not extend beyond the flight-feathers and their principal coverts, as may be seen on p. 290, *l. c.*, pars. 9 & 10.

The next important memoir which appeared is that of Dr. Gadow (20), which throws much light upon the physical and chemical aspect of the feather-structure.

Ignoring for the present a number of casual and disjointed observations which have found their way into literature during this interval, we must look for the next really important contribution towards a more orderly knowledge of the conditions determinating the process of moult in birds to that made in 1896 by Dr. Wittmer Stone (44).

Apart, however, from the prominent part which this author has allotted to the main quills and other feather-tracts of the body, the object of his researches principally centres in an elucidation of the relationship of the moult with the seasonal changes of the plumage in as great a number of families, genera, and species of the birds of North America as possible.

With the exception of the entries made on table iii., p. 116, of his work on the relative condition of the smaller land-birds, no information is given about the covert-feathers. To this work I have had to refer repeatedly in my arguments concerning the different parts of the plumage.

Soon after this there appeared in rapid succession articles by John Guille Millais (35), "On the Change of Birds to Spring-Plumage without a Moult" (referring to the Grebe and Dunlin, but principally the Sanderling), and that by Dr. Chapman (13), also on the Dunlin, the Sanderling, and the Snowflake.

In another paper in 1897, this latter author (15) also made some remarks in reply to Dr. Chadbourne's (11) exhaustive account of his observations on the "Spring Plumage of the Bobolink." The last-quoted papers have mostly dealt with the question of colour-change with or without moult.

Works with a more direct bearing upon the morphological features of the wings of birds, and especially their coverts, are those of Goodchild (27), Wray (46), Gadow (21), and Pycraft (38). More recently, again, Chalmers Mitchell (12) and Pycraft (39) have made attempts to arrive at a final solution of the question of Diastataxy. In these two papers, which appeared contemporaneously, the interest attaching to the wing-coverts as the most important factors was accordingly renewed, and is proportionate in amount to the different standpoint taken up by these two last-named authors.

III.—Method of Research.

The practice commonly adopted for the study of the moult is that of observing the changes on birds living in captivity.

Confinement in cages and enclosures, however, as is well known, so greatly alters the natural habits of birds that the information derived from this source is of too uncertain a character to yield reliable results.

As an instance of this contention, I have to mention only the frequent occurrence of the adoption of the plumage of the male by old female birds deprived of the opportunity of pairing. On this point Dr. Fatio (19) makes the following statement (p. 269, *l. c.*):—"Moreover, anyone may have remarked that a bird which has been kept in captivity, or which has been partially deprived of the normal influences acting from without, never attains the perfection of its plumage so completely as the individual which is in a state of freedom" (translation).

Besides, there is abundant evidence for suspecting moult to be affected in those species of birds which are of migratory habits. It is imperative, therefore, to take into consideration the geographical range of such species when inquiring into the subject. To show that this is the case with imported birds, I may quote the following instances which came under my own observation:—

A two-year old *Cacatua roseicapilla* was transferred from Australia to London during the months of October and November. It had just previous to departure entered upon its regular annual moult, in accordance with conditions existing there; this continued during the voyage, and the process was finished at the end of January, which is the normal course for this species. About the month of June, in the same year, this bird, in accordance with the alternating season, entered upon another complete moult, which it terminated in October following, thus undergoing two complete moults (inclusive of flight- and tail-feathers each time) within one calendar year, a totally unnatural proceeding.

The other bird, a six-year old Parrot (*Platycercus eximius*), whose regular period of annual moult in its native habitat is somewhat later, falling within the months of December to March, on account of the wintry conditions prevailing here after its arrival from Australia, suppressed this yearly process altogether till December of the *following year*, which is the month corresponding with the regular conditions for this moult in the southern hemisphere. Its plumage, on account of having been retained for the two consecutive years, was consequently the worse for wear. (See also Böck (5), p. 207, with remark by Dr. Cabanis.)

From these incidents we derive the further information that the latter and older bird adhered to the moulting-season prevailing for the Southern, whilst the former and younger bird, immediately upon transfer, adopted that of the Northern Hemisphere.

Examples like the foregoing will therefore show the significance of the remarks made on this head.

Without doubt a somewhat similar cause must have been responsible for the greatly contradictory results obtained in the case of the "Bobolink," in the researches made into the moult of this migratory species by Dr. Chadbourne (11) on the one hand, and by Dr. Chapman (15) on the other. An inquiry into the geographical range of *Dolichonyx oryzivorus* discloses the fact that this species extends from the north of Carolina, through Texas and Mexico, into the tropical belt of South America north of the Equator. The chances, therefore, are that Dr. Chadbourne's birds, having been procured from a dealer, as he himself states, may have got into the latter's hands from entirely different districts, and probably also from the extreme limits of the geographical range of this species.

The other plan upon which to conduct the study of the moult, namely, that of using the dried material of cabinets, has some equally serious drawbacks. It rarely happens that a complete series for all the stages forms part of a general collection (*cf.* Allen (1), p. 42). Useful no doubt, as this type of material proves to be in providing supplementary evidence in doubtful cases, the different object, however, for which it has been gathered does not, as a rule, recommend it for this purpose (*cf.* also Wittmer Stone (44), p. 109).

My own method (and for which I have good reasons for reliability) has been that of procuring, at regular intervals of one week, several specimens of the species named, from the first signs of moult appearing, throughout the whole period of feather-change.

By this means the birds can be examined at leisure while yet in a perfectly fresh condition. Their further preservation in alcohol is an additional advantage for resulting them at any time when required for a comparison one with another.

This inquiry was conducted on 32 individual specimens, of which number 21 were were males and 11 females. (See Table I. parts *a* & *b*.)

Of this satisfactory series of specimens on which to base these observations, 27 enter into the descriptions. The remaining 5 specimens, nos. 28–32, which represent those received at the end of the moulting-season, may, though they still show traces of incomplete renewal of a few of the feathers of the trunk, for all practical purposes be considered to have acquired the fully developed garb.

The first step taken in the present investigation has been that of measuring singly each flight-feather in both wings of all the individual birds. This procedure, perhaps unnecessary at first sight, has had the advantage of not only demonstrating the numerous individual differences of lengths of these feathers in a given species, but has

also proved to be of no inconsiderable value as a foundation in the compilation of the comparative diagrams for the "Remiges" (see Pls. XXXVI.–XXXVIII.).

These measurements, moreover, have been productive of a number of useful observations, which might otherwise have escaped notice. I may mention, for instance, the case of the almost isolated condition of the development in rapid succession of primary remiges III., IV., and V., which attain their full lengths without having a corresponding equivalent on the cubital portion of the wing (see Chart, Table II., p. 370, and Diagram B, Plate XXXVI., left and right wing, showing the relative growth of the flight-feathers, which are lettered *c*, *d*, and *e* respectively).

This method has further afforded the means for estimating in percentages the reduction in the power of flight through the loss of flight-feathers during the various stages in the moult of the bird (see Table III., p. 374). That the length of corresponding remiges is never alike in any two individuals seems conclusive, and it is enough, for all practical purposes, to ascertain their mean length. These averages were for the *Metacarpo-digitals* or *Primaries*:—

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.
mm.....	135	142	149	159	182	195	205	197	178	96

for the *Cubitals* or *Secondaries*:—

	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.
mm.....	132	127	124	120	115	110	100	95	75	55

Possibly this procedure may appear somewhat artificial, but it has the advantage of at least supplying approximate data for the ultimate length of those remiges which, being in a state of partial development (or frequently shed altogether previous to their replacement), in this way can be made available for exercising a control over the deficiency caused by their loss.

In this examination some standard is necessary; therefore, each flight-feather has been theoretically reduced to the uniform length of 100, which figure represents its full length.

How this works out may be seen by a reference to the diagrammatic representation of specimen No. 1 in Plate XXXVI. (left wing), and further marked A, in the case of primary I., whose actual length is 110 mm. (expressed in the space on the top), whilst its length in proportion to that of the full growth (*i. e.* 135 mm.) (see above) is therefore $\frac{110\times100}{135}$ =81·0, or in round figures 80, which is practically $\frac{4}{5}$ of its ultimate length. Or to take the case of remex X., which is the shortest of the primaries, whose mean length was ascertained to be 96 mm., as shown in specimen No. 25, and further marked K on Plate XXXVIII. (see Table as in former), which represents this particular stage. Since its actual length was 65 mm. and its mean computed at 96 mm., the relative length therefore is, according to the adopted rule, $\frac{65\times100}{95}$ = 67·7, or practically 70—that is to say, $\frac{7}{10}$ of its ultimate length.

Thus, the comparatively slight discrepancies which must necessarily accrue from the adoption of the theoretical, yet more serviceable, equivalents to those of the empirical figures of their actual measurements, can exert no serious influence on the general result of this investigation.

IV.—Explanatory Remarks on the Diagrams on Plates, Tables, and Charts.

From the 27 specimens more generally described, it seemed advisable to make a narrower selection of 12 typical cases for the purpose of diagrammatic reproductions which illustrate the relative stages of that particular phase which each remex pursues during the moult.

In the diagrams allotted to them in Plates XXXVI.–XXXVIII., these specimens have received a special mark in the shape of a Roman capital letter, irrespective of their serial numbers, which latter are those associated with the dates on which they were received. With these the capital letters correspond tolerably well for denoting the successive stages which are marked by a small Latin letter. The reason for this is that some birds commence to moult sooner than others, and in consequence accomplish the moult earlier. For instance, specimen No. 16, marked F (see Plate XXXVII.), of Dec. 19, which repeats stage *g*, precedes No. 14, of Dec. 11, which is marked G (Plate XXXVII.), because this latter specimen has attained the stage of *h*, which represents the growth of remex VIII. at an earlier date. A similar case to the one mentioned is that of No. 24, and further marked M, of Feb. 18 (Plate XXXVIII.), which had to be placed at the end for representing stage *l'*, or the development of cubital V., as the last remex to appear, because it is a more typical specimen in this respect than No. 25, in which the moult of the same quill has been seemingly accomplished though not entered. Otherwise it bears the same date as the latter specimen—a circumstance which is purely accidental, on account of their having been shot together. Both of these, therefore, antedate No. 26, marked L (Plate XXXVIII.), this having been procured on March 4, which represents the stages intermediate between *i* and *k*, which are earlier than that of No. 24, as we have seen.

Many of these specimens being more or less a repetition only of those extracted for diagrammatical representation, or calling for no special remarks, are referred to only in a general way. Their quotients for the relative lengths of remiges in moult are, however, entered, together with those specially selected for illustration, separately in the two parts of Table I.: part *a* for the left and part *b* for the right wing (see pp. 356–359).

The capital letters which the specimens received in Table I., parts *a* and *b*, correspond with those of the diagrams in Plates XXXVI.–XXXVIII. The specimens are arranged in Table I. in the order of the dates on which they were received. The Roman figures placed at the head of the columns specify the order of the remiges for

both the metacarpo-digital and the cubital portions of the wing. The column of cyphers to the right contains the sums total of the amount of all the flight-feathers under moult in each specimen. The cyphers placed at the bottom of the columns are the sums total obtained for each remex itself, their aggregates agreeing with the grand total of the other column in the right-hand corner.

The cyphers on the second line at the bottom show the number of specimens observed for the moult of that particular remex, and beneath these, in opposition to the numerical order of figures of the remiges at the top, are placed the letters referring to the successive phases (*cf.* also diagrams on Plates XXXVI.–XXXVIII.), in alphabetical order, for the remiges of the hand portion. Their corresponding equivalents for the order of the cubitals are designated by dashes, thus: $'\ ''\ '''$.

The symbol O signifies that the remex has been shed, and the dotted spaces are the places still occupied by the old quills.

As already mentioned, a Table has also been provided for the percentages of reduction of power of flight, giving the amount in each specimen, and for each portion of the wing separately, the totals for each wing, and the grand totals for both sides.

V.—Definition of the "Moult."

A. *On "Adventitious Plumage."*

Before a bird assumes the deciduous plumage which is annually replaced in the same manner, viz., by the process known as the "perennial moult," it is provisionally clothed with generally one, though often two liveries, differing both in function and growth. They require careful consideration on account of their genetic importance. The successive liveries are:—

1. An adventitious downy investment of the nestling, or "Embryo-Plumage."
2. A non-deciduous (ontogenetic) garb of the fledgling, or "Annual Plumage."
3. A deciduous (phylogenetic) feathering of the mature bird, or "Perennial Plumage."

It is to the second livery that usually the term "embryo-plumage" is given, chiefly because it produces the first set of quills and contour-feathers (*Teleoptiles*).

In the nestling of *dasypædic birds* a downy covering (*Neossoptiles*) of the body precedes the latter or plumage of the fledgling. The term "embryo-plumage" therefore belongs to this downy adventitious covering: *cf.* Wittmer Stone (44), pp. 115–117, "Number and Times of Moult"; also Fatio (19), p. 258. These down-feathers are the forerunners of the true contour- and covert-feathers, whose places the latter afterwards occupy. They must therefore not be confounded with the downy structures which grow in the interstices between the latter, such as are found in Ducks, Swans, &c.

TABLE I. *a*.—Showing the relative lengths of growth

LEFT

METACARPO-DIGITALS.

Date.	No. & Age.	Sex.	X.	IX.	VIII.	VII.	VI.	V.	IV.	III.	II.	I.
A. Nov. 5 ..	1, ad.	♂	..	..	..	..	..	..	..	0	73	81
„ 5 ..	2, juv.	♂	..	..	..	..	..	19	62	83	100	100
B. „ 14 ..	3, juv.	♀	..	..	..	..	..	13	50	80	100	100
„ 14 ..	4, juv.	♂	..	..	..	..	..	..	11	40	66	70
„ 14 ..	5, juv.	♀	..	..	..	..	23	71	100	100	100	100
„ 19 ..	6, juv.	♂	..	..	..	..	0	65	100	100	100	100
C. „ 19 ..	7, ad.	♂	..	..	..	..	4	90	100	100	100	100
„ 19 ..	8, juv.	♂	..	..	..	..	69	100	100	100	100	100
„ 28 ..	9, ad.	♂	..	..	..	..	..	54	91	100	100	100
D. „ 28 ..	10, ad.	♂	..	..	..	9	71	100	100	100	100	100
E. Dec. 3 ..	11, juv.	♀	..	..	..	0	58	100	100	100	100	100
„ 3 ..	12, juv.	♀	..	..	..	..	60	100	100	100	100	100
„ 11 ..	13, juv.	♀	..	..	..	..	51	100	100	100	100	100
G. „ 11 ..	14, juv.	♀	..	0	2	56	100	100	100	100	100	100
„ 19 ..	15, juv.	♂	..	..	..	19	15	100	100	100	100	100
F. „ 19 ..	16, juv.	♂	..	..	..	48	94	100	100	100	100	100
H. Jan. 1 ..	17, ad.	♂	..	..	33	73	58	100	100	100	100	100
„ 1 ..	18, ad.	♂	..	..	..	24	74	100	100	100	100	100
„ 16 ..	19, juv.	♀	..	..	33	85	100	100	100	100	100	100
J. „ 16 ..	20, ad.	♂	..	..	33	78	100	100	100	100	100	100
„ 29 ..	21, ad.	♂	0	70	100	100	100	100	100	100	100	100
„ 29 ..	22, ad.	♀	..	..	40	82	100	100	100	100	100	100
„ 29 ..	23, juv.	♀	..	..	0	48	87	100	100	100	100	100
M. Feb. 18 ..	24, ad.	♂	..	33	76	100	100	100	100	100	100	100
K. „ 18 ..	25, ad.	♂	67	78	100	100	100	100	100	100	100	100
L. Mar. 4 ..	26, ad.	♂	95	84	100	100	100	100	100	100	100	100
„ 4 ..	27, ad.	♂	67	84	100	100	100	100	100	100	100	100
	Totals ..	..	229	349	617	1022	1601	2212	2414	2503	2639	2651
Number of specimens participating in the moult of respective quills			4	6	11	16	22	25	26	27	27	27
Order of the moults alphabetically expressed			*k*	*i*	*h*	*g*	*f*	(*e*	*d*	*c*)	*b*	*a*

For explanation of Tables on

of the main quills. O=shed to 100=full growth.

WING.

Cubitals.

No.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	Totals.
(1)	..	..	..	..	..	..	..	94	93	..	341
(2)	..	..	..	..	..	..	..	78	100	..	542
(3)	..	..	..	..	..	..	..	57	20	..	420
(4)	..	..	..	..	..	..	..	52	20	..	259
(5)	15	..	..	..	..	..	..	100	100	9	718
(6)	34	..	..	..	..	..	..	100	93	..	692
(7)	45	..	..	..	..	..	25	100	100	45	846
(8)	87	..	..	..	..	..	100	100	100	100	1056
(9)	37	..	..	..	..	..	100	100	100	100	882
(10)	68	0	..	..	..	0	75	100	100	0	923
(11)	87	43	..	..	..	..	100	100	100	81	1069
(12)	94	51	13	..	..	..	40	100	100	81	1039
(13)	90	47	..	..	..	..	20	100	100	100	1008
(14)	100	100	38	..	..	..	40	100	100	100	1236
(15)	94	27	..	..	..	..	100	100	100	0	955
(16)	100	94	24	..	..	..	60	100	100	90	1210
(17)	100	100	80	20	..	..	40	100	100	100	1304
(18)	100	70	20	..	..	..	80	100	100	100	1168
(19)	100	100	92	8	..	..	100	100	100	100	1418
(20)	100	100	92	37	..	..	100	100	100	100	1440
(21)	100	100	96	100	..	..	100	100	100	100	1666
(22)	100	90	40	..	..	..	100	100	100	100	1352
(23)	64	51	..	..	..	..	..	100	100	54	1004
(24)	100	100	100	100	78	100	100	100	100	100	1787
(25)	100	100	100	100	100	95	100	100	100	100	1940
(26)	100	100	100	91	13	100	100	100	100	100	1883
(27)	100	100	100	100	?	60	100	100	100	100	1811
	1915	1373	895	556	191	355	1580	2581	2526	1760	29969
	23	18	13	8	3	4	20	27	27	22	Grand Total.
	f'	*g'*	*h'*	*i'*	*l*	*k'*	*f''*	*a'*	*b'*	*f''*	

pp. 356–359, see pp. 354, 555.

TABLE I. *b*.—Showing the relative lengths of growth

RIGHT

CUBITALS.

Date.	No. & Age.	Sex.	X.	IX.	VIII.	VII.	VI.	V.	IV.	III.	II.	I.
A. Nov. 5 ..	1, ad.	♂	..	93	73	..	..	..	..	..	..	..
„ 5 ..	2, juv.	♂	..	100	84	..	..	..	..	..	..	..
B. „ 14 ..	3, juv.	♀	..	40	68	..	..	..	..	..	..	..
„ 14 ..	4, juv.	♂	..	33	57	..	..	..	..	..	..	..
„ 14 ..	5, juv.	♀	..	100	100	..	..	..	..	..	..	11
„ 19 ..	6, juv.	♂	..	86	100	..	..	..	..	..	..	33
C. „ 19 ..	7, ad.	♂	..	100	100	..	..	.	..	..	..	34
„ 19 ..	8, juv.	♂	100	100	100	100	..	..	..	..	..	98
„ 28 ..	9, ad.	♂	100	100	100	100	..	..	..	..	..	37
D. „ 28 ..	10, ad.	♂	100	100	100	25	..	..	..	..	0	71
E. Dec. 3 ..	11, juv.	♀	81	100	100	100	..	..	..	..	39	83
„ 3 ..	12, juv.	♀	81	100	100	15	..	..	..	..	35	94
„ 11 ..	13, juv.	♀	27	100	100	100	..	..	..	..	35	83
G. „ 11 ..	14, juv.	♀	0	100	100	45	..	..	..	36	100	100
„ 19 ..	15, juv.	♂	100	100	100	90	..	..	..	..	30	90
F. „ 19 ..	16, juv.	♂	36	100	100	50	..	..	..	12	90	94
H. Jan. 1 ..	17, ad.	♂	100	100	100	0	..	..	20	72	100	100
„ 1 ..	18, ad.	♂	100	100	100	40	..	..	..	0	90	100
„ 16 ..	19, juv.	♀	81	100	100	100	..	..	2	92	100	100
J. „ 16 ..	20, ad.	♂	100	100	100	100	..	..	33	92	100	100
„ 29 ..	21, ad.	♂	100	100	100	100	..	..	..	56	100	100
„ 29 ..	22, ad.	♀	100	100	100	100	..	..	..	36	100	100
„ 29 ..	23, juv.	♀	72	100	100	..	..	..	..	..	39	98
M. Feb. 18 ..	24, ad.	♂	100	100	100	100	100	52	100	100	100	100
K. „ 18 ..	25, ad.	♂	100	100	100	100	95	100	100	100	100	100
L. Mar. 4 ..	26, ad.	♂	100	100	100	100	100	13	95	100	100	100
„ 4 ..	27, ad.	♂	100	100	100	100	90	?	100	100	100	100
	Totals ..	..	1678	2552	2582	1465	385	165	450	796	1358	1926
Number of specimens participating in the moult of respective quills			20	27	27	19	4	3	7	12	18	23
Order of the moult alphabetically expressed			*f''*	*b'*	*a'*	*f'''*	*k'*	*l*	*i'*	*h'*	*g'*	*f'*

of the main quills. O=shed to 100=full growth.

WING.

METACARPO-DIGITALS.

No.	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	Totals.
(1)	62	63	O	..	..	..	..	.	..	..	291
(2)	100	100	90	75	35	..	..	..	..	..	584
(3)	100	100	83	59	24	..	..	..	..	..	474
(4)	66	59	40	3	..	..	..	..	..	..	258
(5)	100	100	100	100	71	23	..	..	..	..	705
(6)	100	100	100	97	63	O	..	..	..	..	679
(7)	100	100	100	100	87	38	..	..	..	..	759
(8)	100	100	100	100	100	71	..	..	..	..	1069
(9)	100	100	100	88	54	2	..	..	..	..	881
(10)	100	100	100	100	100	74	2	..	..	..	972
(11)	100	100	100	100	100	58	O	..	..	..	1061
(12)	100	100	100	100	100	56	..	..	..	..	981
(13)	100	100	100	100	100	64	7	..	..	..	1016
(14)	100	100	100	100	100	100	56	2	..	..	1139
(15)	100	100	100	100	87	69	12	..	..	..	1078
(16)	100	100	100	100	100	92	48	..	..	..	1122
(17)	100	100	100	100	100	100	73	33	..	..	1298
(18)	100	100	100	100	100	87	29	..	..	..	1146
(19)	100	100	100	100	100	100	97	60	..	..	1432
(20)	100	100	100	100	100	100	82	35	..	..	1442
(21)	100	100	100	100	100	100	97	76	5	..	1434
(22)	100	100	100	100	100	100	75	35	..	..	1346
(23)	100	100	100	100	100	87	51	O	..	..	1047
(24)	100	100	100	100	100	100	100	81	19	..	1752
(25)	100	100	100	100	100	100	100	100	75	67	1937
(26)	100	100	100	100	100	100	100	86	50	..	1744
(27)	100	100	100	100	100	100	100	100	75	67	1832
	2628	2622	2513	2422	2221	1721	1029	608	224	134	29481
	27	27	27	26	25	23	17	11	5	2	Grand Total.
	a	*b*	(*c*	*d*	*e*)	*f*	*g*	*h*	*i*	*k*	

Fatio (*l. c.* p. 252) mentions them as "Première livrée de l'enfance," &c. From the same author we also learn that the existence of the down-feathers is very brief, even in those birds whose nestlings retain them during the earlier stages of development, until their actual fledgling-plumage appears.

Structurally, these feathers belong to the filo-plumaceous type (Fatio, pp. 252–254, *l. c.*), giving the young bird the somewhat *silky*[1] appearance of which Fatio speaks.

The filo-plumaceous feathers are either pushed or borne out on the tips of feather-papillæ of the more specialized plumage which follows on. This is formed in the corium. The duration of attachment of the first livery to the new feathers varies considerably; it also varies according to families. (See also Fatio, *l. c.* p. 263.)

In some it is repeated through every feather-change, as in the *Struthionidæ*. In the greater part of the *Carinatæ* this sessile condition is confined to the first change. Cases of three simultaneous attachments of feathers are known to occur occasionally, of which one is mentioned by Wittmer Stone (44), p. 112, for a Meadow-Lark. This author also quotes the case observed by Will. Palmer in the 'Auk,' 1894, of a young Hooded Warbler, *Sylvania mitrata*, in which the *down*[1] of the nestling was to be seen at the tip of the feather of the first plumage, while the latter was "*in turn attached*[1] to the new feather of the winter plumage."

In Struthious birds this latter phase seems to be of frequent occurrence, as I myself have found several instances in the Emu (*cf.* also Fatio, *l. c.* p. 253). These filamentous sessile plumes are to be seen in a young *Columba domestica* figured by Pycraft (39), plate xvi. fig. 1, where they are supported by the main coverts which are sprouting, and reference may also be made to my figure of a young Parrakeet (*Platycercus eximius*) (see text-figures 1 & 2), where they are clearly defined for all the series of coverts and contour-feathers.

I have not myself had the good fortune of proving the existence of these plumes on the rectrices, but an observation was made by Brehm (8), p. 346, on this point in the Owls, whose remark on it in the original is as follows:—

"Die einjährigen Vögel erkennt man übrigens doch *untrüglich* daran dass die *Spitzen ihrer Steuerfedern*, weil der *Nestflaum auf ihnen gesessen hat*, eine *kleine Lücke* in der *Mitte zeigen*"[1].

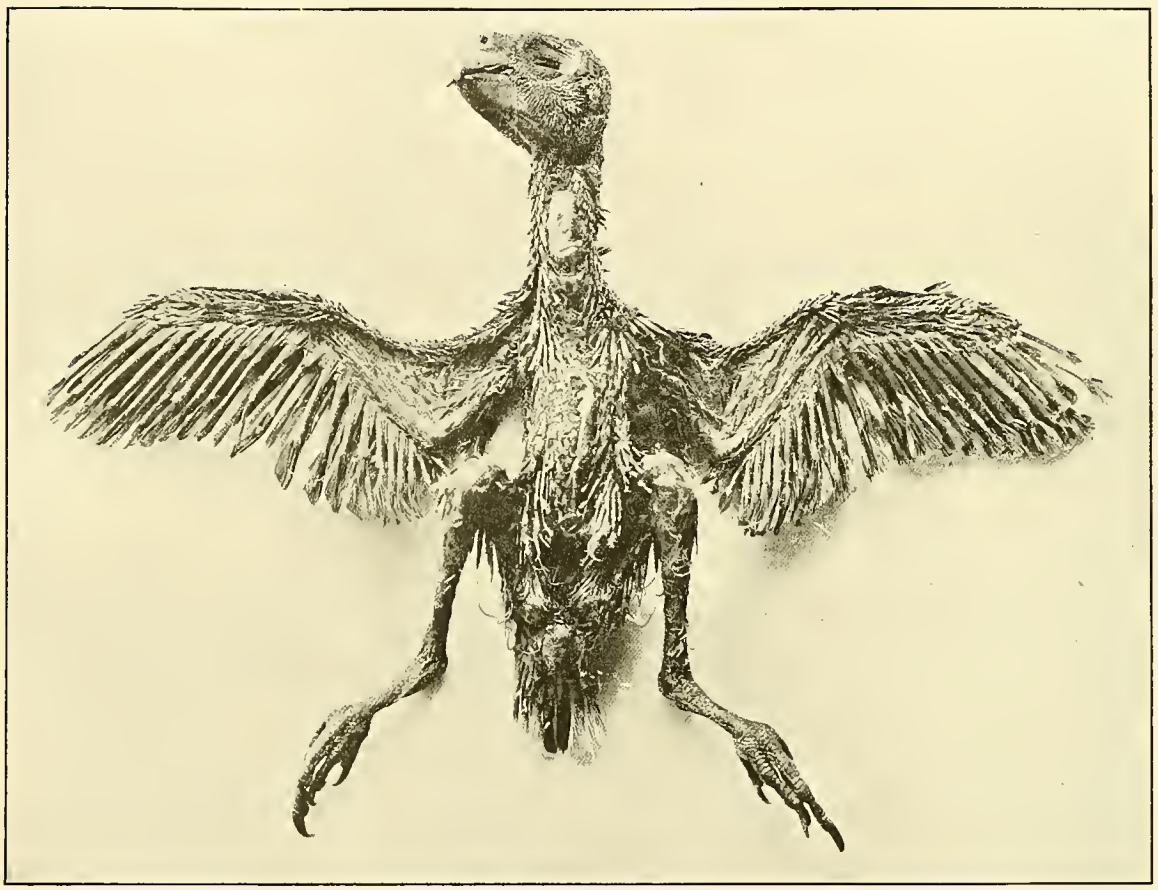
The important nature of this passage resulted in a footnote from the Editor (Dr. Cabanis) to the following effect:—"Eine etwas *suptile Wahrnehmung*," &c.; and further, "die ober wohl beachtens werth scheint und jedenfalls wiederum von der anerkannt *scharfen Beobachtungsweise des Verfassers zeugt*"[1].

Yet the *nicety* of this observation of Brehm, as pointed out by Dr. Cabanis, gains in strength materially if we turn to a statement made by Blyth (4), who, on p. 260, in

[1] The *italics* are mine.

referring to the feather-changes in general, says :—" In the Widgeon, however, and many other species, it will be found that the adult livery is obtained, in spring, by an actual change of plumage, every feather being cast and renewed, except, of course, the *wing* and *tail-primaries* [1]. And here it may be remarked that the *two central caudal feathers* [1], which in all birds visibly differ from the rest, being of softer texture

Text-fig. 1.



Young Parrakeet, showing the filamentous plumes (neossoptiles) carried on the tips of the new contour-feathers.

and commonly of another colour, *partake of the nature of the tectrices and wing-coverts* [1], and in double-moulting species are, like them, very usually shed and renewed with the vernal renovation of clothing-plumage," &c., &c.

Now, whether or not, Brehm, in his observation of *Syrnium*, using the general term of " rectrices " (Steuerfedern), had in mind the two centrally situated caudals only, does not appear ; in any case, it would seem that so far Blyth's observation of the value of these was fully confirmed.

[1] The *italics* are mine.

If it could be shown that the "primary" value of feathers could be established by Brehm's observation, we should become possessed of a good test for their serial value. Having paid attention to this feature whenever a favourable opportunity presented itself, in no case have I met with the sessile condition of these early plumes on the flight-feathers, though they are present invariably on the main coverts, both dorsal and ventral, according to my observation.

If, so far, we are supplied with even this slight means of differentiation between the remiges and the rest of the covert- and contour-feathers, then we should have ample proof that the principle of specialization, at any rate for the flight-feathers, is carried out perceptibly early in the life of the bird; and this differentiation seems to be of considerable genetic importance. Moreover, there is the well-known fact of the unvarying absence of after-shafts in the case of both categories of flight-feathers.

It should be pointed out that Brehm (7 & 8) in his article, besides mentioning this mode of replacement for the first plumage, also instances, by again referring to the genus *Syrnium*, this peculiar condition as taking place during the second annual moult. A repetition of this kind of renewal then naturally leads to the assumption of a primitive condition of the plumage, to which the soft and downy feathering of the Owls certainly points. And if we were to apply the existing analogy to some of the *Ratitæ*, the theory as to their descent from a bird which once possessed the power of flight (Gadow (21), p. 667, quoting Fürbringer) is not the less tenable on account of their body-plumage still retaining this primitive style of feather-production, seeing that such a combination still exists for the Owls.

I may mention here that owing to the yet more primitive conditions of the feathers on the trunk in some of the *Ratitæ*, the extreme tips of the after-shafts, which in the Cassowary and the Emu attain a length equal to that of their main shafts, *jointly support the new-growth feather* [1] with the latter.

Necessarily this throws a curious side-light upon the structure of the feather in the Struthiones, as Beddard (3), p. 18, rightly suggests, under the heading "Pterylosis," by concluding that "The feathers of those birds have been called intermediate between contour-feathers and downs. *It may be that they are primitive* [1], and that the struthious birds have arisen from some ancient type *in which the modern bird's feather had hardly been evolved*" [1].

To a great extent, then, will this help to solve the true relationship of the after-shaft to the main shaft (*cf.* also Nitzsch (37), pp. 8 & 9). The importance attaching to the bifurcated follicle, as shown in the beautifully executed drawing of its desiccated cells, known as the "soul" in the quill by Holland (29), on table i., figs. 2 *b* & 3 *b*, becomes at once fully apparent. Their union occurs in the *cavum calami* within the "*corpus calamus*," of which the one branch deposits the *substantia rhachidis externa* for the

[1] The *italics* are mine.

main, and the other the same substance required in the building-up of the after-shaft. In speaking of the latter, Holland, on p. 346, *l. c.*, says: "Bei Federn mit Afterschaft bildet sich dem ersten gabelförmigen Streifen gegenüber am Bauche des *folliculus* noch ein zweiter ähnlicher Längsstreifen, an denen dieselbe Bildung vorgeht, wie wir eben gezeigt, und der *folliculus* lagert nach seiner vorderen und hinteren Seite Mark ab. *Wo das corpus calami beginnt verwachsen beide Schäfte zu Spule*" [1].

Any doubts existing as to the structural plan of the primitive contour-feathers are dispelled consequently by the retention in the Cassowary and the Emu of the original feather-structure. *This was a duplicated organ* (see also Nitzsch, p. 9), *of which the two component parts*—in the birds alluded to—*are still of equal length and strength* [1]. These latter qualities are carried out to such a point of perfection that it is really difficult to determine which is the *rhachis* and which the *hyporhachis* [2].

For the reduction of the latter (to $\frac{2}{3}$ the length of the main shaft in the Grouse), to its total disappearance, we get every degree of perfection in the development for the main shaft of the feather towards that highest of degrees, as attained by the *Oscines* amongst the Passerine birds at the expense, as it were, of the after-shaft. This more highly specialized and simple form of feather, as acquired in recent types of birds for perfected adaptation to flight, is then really only one-half of the feather, and, however incongruous the inference may be, is a degeneration from the original duplex structure.

B. *On the "Feathering of the Fledgling."*

A probably common feature of all the Carinatæ is the mode in which they acquire the first set of flight-feathers. The supply of this first set of quills on the wing is generally concurrent with the appearance of the greater portion of the contour-feathers in the principal tracts of the trunk and on the head.

In the *Gymnopædes* the remiges appear somewhat in advance of the latter. They also appear simultaneously with the upper major coverts by practically the whole series shooting out along the posterior margin of the fore limb and in synchronism (see text-figure 2, p. 364, of young Parrakeet). Indeed, the upper major coverts even precede the remiges in some birds, judging from a statement made and figures given by Pycraft (39) (*cf.* footnote, p. 251, & pl. xvi. fig. 1, *l. c.*) in the case of the young of the Common Fowl and that of a Pigeon. This I can also confirm from my own

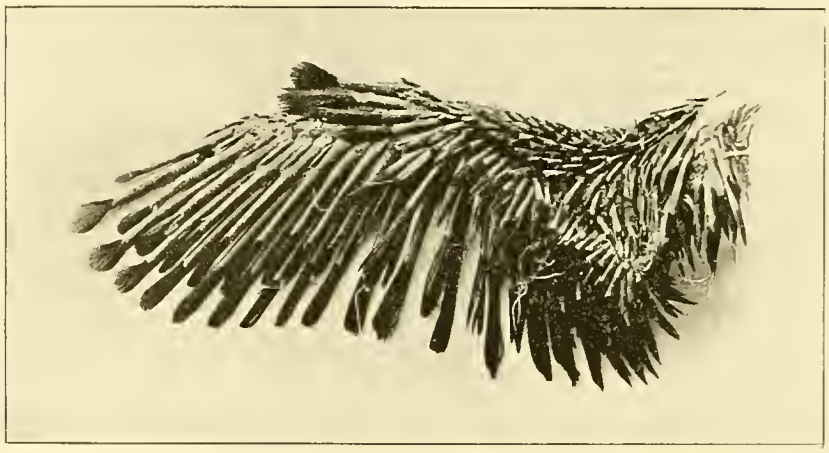
[1] The *italics* are mine.

[2] In feathers of equal lengths for the two parts, such as in the Emu, it can be reliably ascertained only when *in situ*. As a symmetrical structure consisting of two equivalent parts, it naturally follows that their ventral or, more correctly designated, *inner sides* face each other, whilst the outer sides (dorsal for the main, ventral for the accessory feather) are averted, irrespective of the convexity of their surfaces, which is a concentric one for both.

observation. This mode of a first acquisition of flight-feathers equally applies to the rectrices.

The birds known as *Nidifugæ*, like the *Gallinæ* and most of the game-birds, acquire their flight-feathers shortly after emerging from the egg. The young of the Argus Pheasant is an instance in which flight-feathers make their appearance immediately upon leaving the egg. But we have evidence of much earlier development of flight-feathers than that mentioned above. This is seen in the *Megapodes* (and very probably too amongst the *Cracidæ*), whose young acquire their first set of remiges *before* [1] they leave the egg. To this character the term of "*Ovifugæ*" might reasonably be given. Whether or not this first plumo-pennaceous garb be præ- or post-incubate, matters little; it invariably is heralded in the *Dasypœdes* by the adventitious plumage referred to above as the truly embryonic one.

Text-fig. 2.



Dorsal view of the left-side wing of a young Parrakeet, showing the sessile filamentous plumes of an adventitious plumage (neossoptiles) on the tips of the upper covert-feathers.

The function of the first set of flight-feathers with their principal coverts in the fledgling being practically the same as that in the more matured individual, structurally it is, nevertheless, inferior and more primitive in texture than that acquired by subsequent moults. The vanes of the feathers are generally broader, their tips more rounded, the barbs and barbules present a looser union than those which eventually replace them (see remarks made on this point by Brehm (7, 8), also Fatio (19), p. 254). The body-feathers are similarly inferior in substance. Wittmer Stone (44), on pp. 115–117, makes the following statement:—"The remiges and rectrices of the first plumage are usually the same as those of the adult, *but the body-feathers*, while of the ordinary structure, *are much more plumulaceous* [1] than the covering of the adult"—deficient

[1] The *italics* are mine.

not only in warmth of colour, but also in that lustre which imparts to them a finish which makes them distinguishable even to the "touch alone" from the adult birds (Altum (2), p. xxi). In a word, it is a provisional plumage.

Its duration, according to the quotations of the different writers, seems to vary for the families, the genera, and also for the different species amongst the latter; but on this head, owing to observations being frequently based on unreliable material, there is great confusion.

According to Brehm (8) this first or fledgling-plumage is replaced in the genus *Strix* by another of similar primitive quality—an observation which again called for a foot-note from Dr. Cabanis (p. 344, *l. c.*), in which he gives expression of genuine surprise in the following manner:—"*Also zwei Dunenkleider!*"[1] &c., &c. "*Das ist in der That sehr bemerkenswerth*," &c. But Brehm also showed that in the young of the *Owls* the flight- and the tail-feathers, as well as the body-feathers, are shed in the same season in which the bird was hatched, while in the *Birds of Prey* only the body-feathers, excluding the remiges (and probably, too, the tectrices), are shed, these latter being shed in their second autumn (Brehm (7), p. 196, & (8), p. 345). This statement of Brehm was published only a year after the one in which Schlegel (40) made the sweeping assertion that "*the young birds moult for the first time in the autumn of that year which follows the one in which they were born*"[1]. As the aforesaid statement formed one of the fundamental tenets of Schlegel's theory for the alleged regeneration and revitalization of the bird's feathers, it should scarcely be surprising to find that no sooner had it been published than it drew a host of contradictions, not only from Brehm, but also from the ablest observers amongst ornithologists of the time. Amongst the latter was Homeyer (30 *a*), who, after enumerating a considerable portion of the birds composing the list of genera and species claimed by Schlegel for changing colour *without* moult, irrevocably proved this colour-change *with* moult by emphasizing on p. 117 of the article, under the heading of "allgemeine Grundzüge," &c., on the first feather-change in the following conclusive words:—"6. Alle kleineren und viele grössere junge Vögel *mausern vollständig im ersten Herbste ihres Lebens*."

My own observation also disproves Schlegel's statement in regard to this wholesale assertion. To the list, therefore, of birds which undergo their first total moult in the season in which they are reared, I can add also *Gymnorhina tibicen*, the species which has been under my particular consideration and upon which I base this paper.

C. *On "Perennial Feathering."*

The manner in which the feathers on the wing of a fledgling bird are replaced in subsequent changes is strikingly different from that in which they acquired them at

[1] The *italics* are mine.

first. It differs from it in shedding and eventually substituting the quills one by one, sometimes two, even three or four at a time, occasionally but rarely more. Some exceptions to this rule occur amongst the *Chenomorphæ* (Schlegel (40), p. 20, *l. c.*, also mentions the *Anatinæ* as exceptions), where the juvenile condition of shedding the flight-feathers in greater numbers seems to occasionally recur with the periodical moult. A case of such a seemingly abnormal character has been observed by Wiese, on an old Crane ("Beiträge zur Ornithologie Pommern's," J. f. O. 1855, iv. Heft, No. 18, p. 515). But, as has been pointed out by Gloger (26), p. 392, when remarking on this case: "These birds have other means of locomotion than flight alone." Quite recently I had an opportunity of seeing a like condition in a Moorhen, kindly brought to my notice by Mr. C. H. Grant in the Natural History Museum, who regarded the occurrence as an exceptional one. The fishermen of the lake-entrances and inlets on the south coast of Australia know this fact so well that in the case of the Black Swans (*Chenopis atrata*), which are so numerous there, they frequently take advantage of the temporary impediment to which the "Moulter," as the bird is called at this time, is subjected, and amuse themselves by running it down in their sailing-craft—a very exciting sport.

With regard to perennial moult, Schlegel (40) says, p. 20: "6. The order in which the flight-feathers are shed and replaced is that of bilateral symmetry." Beyond this general statement he has nothing further to say with regard to this important factor in the feather-change. The observation that the flight-feathers were replaced in an irregular sequence of their order, belongs to Gerbe (23). Although his observations extended to a general comparison only between the *Gallinæ* and *Passeres*, it is noteworthy, nevertheless, to find how greatly he was struck by the peculiarity of order in which the moult proceeds on the forearm. This order he describes thus: "7°. A l'avant-bras, la mue chez les Passereaux ne commence généralement que lorsque la cinquième des primaires vient de tomber. *Elle se manifest à la fois sur les deux points extrêmes du cubitus et prend deux directions qui tendent l'une vers l'autre*[1]: d'un côté elle se poursuit de la première de *secondaires* (*cubitals*)[1] à la sixième inclusivement; de l'autre de la neuvième ou dernière à la septième."

For a considerable extension of our knowledge on this point we are indebted to the researches made by Wittmer Stone (44), who regards the laws and principles which govern ecdysis as, what he rightly terms for the bird, "*a physiological necessity, common to all*"[1]. But in attempting to deal with it in general as he has done, the ground cannot be considered as sufficiently prepared until all the phases are known through which the individual passes.

[1] The *italics* are mine

VI.—"Orders of the Moult" in *Gymnorhina tibicen*.

A. *Flight-feathers or Pennæ alares = Remiges primores plus Remiges cubitales* (Sundevall).

The relative lengths of the flight-feathers on the manus are in the order below from left (the longest) to right (the shortest), thus:—

7—6—8—5—9—4—3—2—1—10.

The manner in which the remiges make their appearance is regulated by a definite order in both portions of the wing. As might have been expected, the bilateral symmetry assigned for the individual (*cf.* Schlegel, 40, p. 21) is not strictly observed. But there is at no time any considerable departure from the broad principle. Besides this general bilateral form of symmetry, there is one existing also for the two portions of each wing *inter se*, viz. the hand and the forearm. It is present during the earliest stage of the moult in the case of primaries I. and II. and secondaries VIII. and IX., the remiges corresponding with each other for moulting first, as represented by specimen No. 1.

Diagr. A (stage *a* and *b*). (Lettered on Plate XXXVI. *a*, *b* and *a'*, *b'* respectively.)

The fully adult specimen No. 1 (left and right wing) showed this earliest stage remarkably well; younger ones not complying with the rule so exactly, as No. 2 proves, and also the following one, shot on the same date, mostly young birds.

Diagr. B (stage *c*, *d*, *e*). (Plate XXXVI.)

The parti-lateral symmetry of the first stage becomes soon disturbed by the appearance, in rapid succession, of primaries III., IV., and V., lettered in the Table *c*, *d*, and *e* respectively, *these having no equivalent renewal on the cubitus*[1]. Four specimens show this arrangement remarkably well, of which No. 4, a very young male, does so in part only. The diagram represents specimen No. 3.

Diagr. C (stage *f*). (Plate XXXVI.)

The next stage, that of *f*, which comprises the replacement of primary VI., is a particularly interesting one, insomuch as it marks the restoration of the parti-lateral symmetry by an almost simultaneous development of three secondary remiges. These are cubital remiges I. or f', X. or f'', and VII. or f'''. *Their synchronous appearance therefore is a compensation for primaries*[1] III., IV., and V. It is marked best in the left wing of specimen No. 7, Plate XXXVI., as shown in the diagram C, which represents this third stage or that of *f* and its equivalents. This also explains the reason why these remiges are equivaluated f', f'', and f''' respectively (the dashes representing

[1] The *italics* are mine.

their sequence of growth), and not, as one would have expected c', d', and e', were they making their appearance in synchronism with c, d, and e. Four specimens show this phase of moult, viz. Nos. 7 (diagr. C, Plate XXXVI.), 8, 9 (partially in arrear), and 10 (see also Plate XXXVI., diagr. D), partially in advance of development. So well, however, does the latter one (No. 10) mark this stage and also the following, viz. that of g in its beginning, which latter is the moult of primary VII., that it has been added also to the series of diagrams, in which it is marked D, as illustrating a case of transition for the two stages.

Diagr. D, showing transition between stages f' and g. (Plate XXXVI.)

This represents specimen No. 10, and referred to above. This individual is very asymmetric in moult, both for bilateralism and left-sided development. It exhibits the somewhat rare occurrence on its left-side cubitus of synchronously shedding no less than three remiges: viz. X. belonging to stage f', II. stage g', and very prematuredly VI., as belonging to a much later stage, *i. e.* that of k'. Its right side fairly agrees with the normal condition.

Diagr. E (stage g). (Plate XXXVII.)

Stage g, or the replacement of metacarpo-digital remex VII. and synchronous in growth with cubital remex II. (g') (as referred to for the last specimen, No. 10), is not clearly defined in either of the five or six individuals which share this phase of the moult. For instance, in No. 12 this phase is shown in the cubital portion only; while in its hand portion the changes are in progress only as far as remiges VI. on both sides. Similarly No. 13 for its left side, while the right side of this specimen shows stage g in a normal condition.

An otherwise clear case of this stage of development obtains for specimen No. 15; but this individual, being a later acquisition than No. 14, which represents a typical case of the next following phase, or that of h, I have consequently not admitted to the diagrams, because of the desirability for conforming to the order in the succession of the dates as near as possible.

Specimen No. 11 therefore has been substituted to supply the present *Diagr. E*, Plate XXXVII., as supplementing the part development of this stage of g, referred to in the previous diagram D.

Diagr. G (stage h). (Plate XXXVII.)

The next phase in the moult is that of metacarpo-digital remex VIII., or stage of h, which appears in regular sequence in the numerical order of the feathering of the hand portion. Corresponding in synchronous development on the cubitus with this quill is remex III., lettered h'.

As mentioned above, specimen No. 14 shows this phase distinctly, though in its

early growth. This is particularly the case for the primaries, on both sides, which are just issuing; whilst cubital remiges III. have already attained about $\frac{1}{3}$ of their ultimate lengths. Being, however, developed quite symmetrically, the specimen was better adapted for a concise diagrammatic representation of this stage than other and later ones, which blend more or less with either the earlier stage of *g* or the later one of *i*.

Diagr. F (supplementing stages *g* and *h*). (Plate XXXVII.)

The specimen which supplies this diagram is No. 16. It is one showing the phases of transition between *g* and *h*. This specimen repeats and completes the stage of *g*, while that of *h* is developed in part. It therefore precedes for stage of development of specimen No. 14, diagr. G, on the same Plate, although forming part of a complement of specimens which were received at a later date.

Diagr. H (illustrating stage *i* partially). (Plate XXXVII.)

In specimen No. 17, which this diagram represents, we have an individual which should mark the next phase in the moult of the primaries, namely that of metacarpo-digital remex IX. or *i* if under normal conditions. But this individual being in arrear of moult for the hand portions (metacarpo-digital remiges IX. being as yet undeveloped) it merely shows this phase of renewal for their corresponding remiges IV. or *i'* on the cubitus. It has been diagrammatized, nevertheless, for helping to complete the illustration of this stage of development, which is one not very clearly accentuated in either of the specimens which partake of it. For instance, Nos. 18 and 19 are considerably in arrear of moult; the latter, however, is distinguished by showing stage *i* partially on the cubitus. No. 20 agrees with No. 19.

Diagr. J (supplementing stage *i*). (Plate XXXVIII.)

In specimen No. 21, which this diagram represents, we have a case in which the conditions for stage *i* are reversed: since remex IX. is in full process of growth in the hand portion of the left wing; whilst it has just issued on the right wing, the side in which it is usually more in arrear than the other. The moult for cubital remex IV. or *i'*, the corresponding one for that of the hand portion, has not yet set in for the right side. This specimen, then, together with that shown in *Diagr. H* (the former one), supplement each other in the completion of stage *i* and *i'* respectively.

No. 22, in arrear of moult, conforms to stage *h*, but is conspicuous as showing a case of almost perfect bilateral symmetry.

No. 23 is further in arrear, having reached stage *g* only.

Diagr. K (stage of *k*). (Plate XXXVIII.)

In specimen No. 25 the successive growth of metacarpo-digital remex X. or stage *k*, and the last to be replaced for this series, we possess a particularly well-defined case of absolute bilateralism of symmetry. The development of this flight-feather has reached exactly the same length on both sides. Its synchronous equivalent on the cubitus, namely remex VI. or *k'*, has also been developed in perfect symmetry, having nearly obtained its full growth. The metacarpo-digital remiges IX., also symmetrically developed on both corresponding portions of the wings, are yet incomplete, though porportionately further advanced than X., and beautifully show the regular order of their successive growth. This particularly typical specimen deserves special attention.

A glance at the diagram of this last specimen will at once disclose the fact that the replacement of the flight-feathers, which at this stage is merely completed for the hand portions, is incomplete for the cubitus, where a gap is left still for the filling in of remex V., which is the last one to appear in this section of the wing. The earlier accomplishment of the moult of the flight-feathers belongs, therefore, to the hand portion, both in its initiating as well as its concluding stages. This is the case with three specimens out of four which participate in this last phase. These are Nos. 24, 25, and 26 (left wing), and which have all been diagrammatized chiefly for showing the growth of cubital remex V. in its earliest relationship to the others; and lastly, No. 27, which also shows a further case of perfect bilateral symmetry. It has been found necessary to give a diagram of No. 24, because it shows the final stage in filling up the gap by cubital remex V. Again, this stage, having practically no synchronous equivalent on the hand portion as above mentioned, required the application of the additional letter *l'* to mark this supernumerary condition.

Diagr. L (stage of *l'*). (Plate XXXVIII.)

This represents specimen No. 26, and shows this stage in its beginning, the secondary remex V. being of equal development on both wings.

The growth of primary X. is nearly complete for the left wing; whilst its development on the right side is considerably retarded.

Diagr. M (supplementing stage of *l'*). (Plate XXXVIII.)

As indicated above, specimen No. 24, though imperfect for the completion of the moult on its hand portion, but otherwise very symmetrically developed, forms a case for further progress in the final stage of *l'* or cubital remex V. It is curious to note how early this specimen has reached this stage, being of February 18th, when compared with 26th and 27th, which were both received a week later, namely March 4th.

As already stated, the specimens completing the List of Birds examined, which were received as late as the end of April, had their moult positively completed,

[*To face* p. 370.

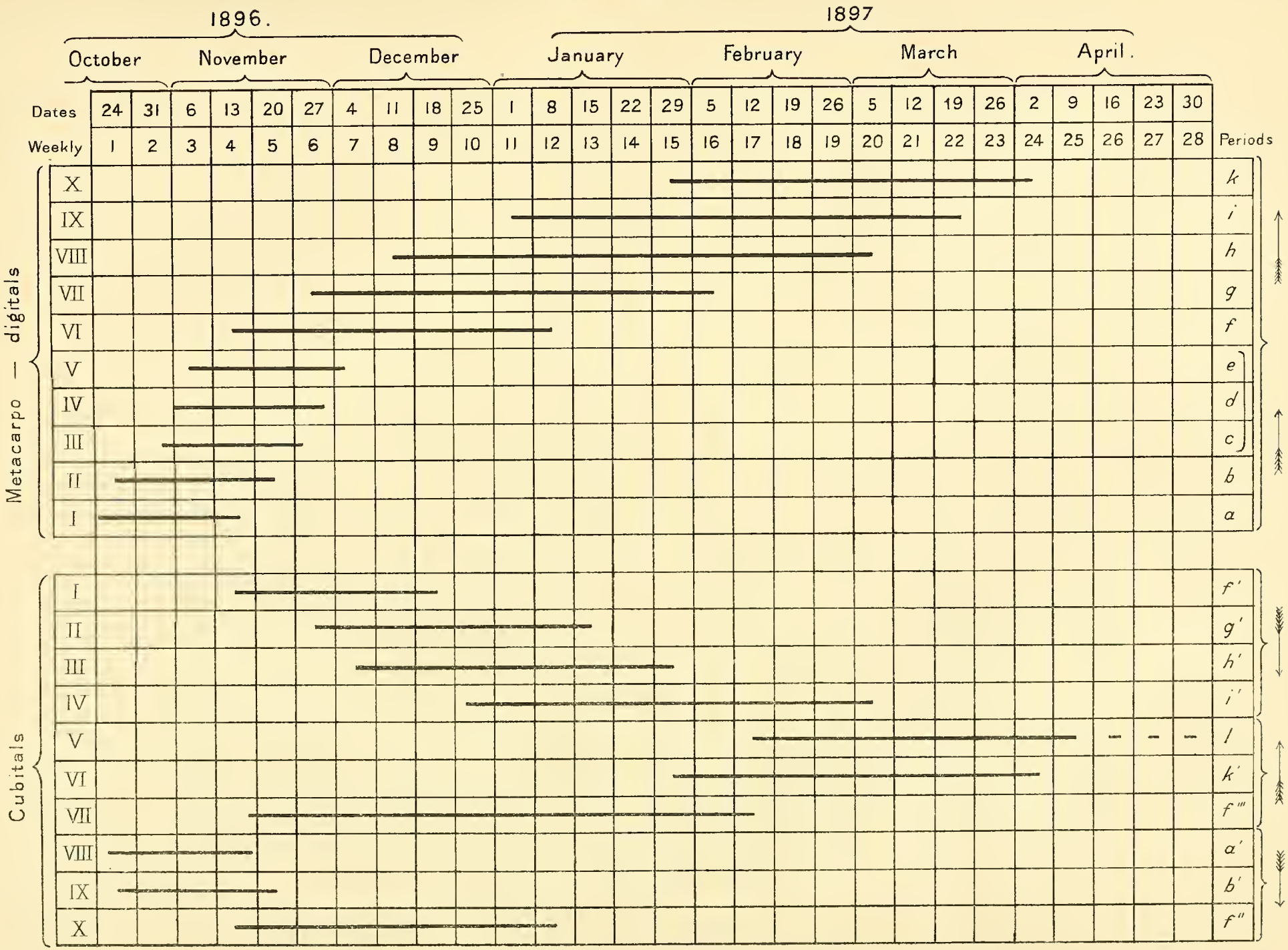
EXPLANATION OF TABLE II.

1. The *vertical lines* form the divisions for the whole period of the moult for the remiges, consisting of 28 weeks.
2. The *horizontal bars*, situated between any multiple of vertical lines, represent the respective remiges, whose ordinal number, in Roman figures, is placed in the lefthand-side column, as counted from the wrist-joint.
3. The letters to the right side of the table denote the order in which they moult, by plain letters, and alphabetically arranged for the metacarpo-digital—with one or more dashes (thus, ′, ″, ‴) for the cubital portion of the wing, and also in their synchronizing order of moult with that of the hand-portion.

   The *darts* on the right side of these letters are indicative of the direction of their moult for the groups of which these remiges form an integral part. (See also Plates.)
4. *Top line*: names of months for the period during which the perennial moult of the flight-feathers proceeds in *Gymnorhina tibicen*.
5. The *numbers* entered on the *second line* are the dates of those months on which the specimens were received and examined.
6. The cyphers on the *third line*, in addition to the number of weeks which each particular quill requires for its development (collective time for the species) from its first appearance to its full growth, also serve for comparing chronologically any two or more quills between the metacarpo-digital and the cubital portion of the wing, or *inter se*.

To face p. 370.

TABLE II.



E. Degen, del.

Bale & Danielsson, Ltd.

Chart, setting out the Period of Growth, and Chronology in the Development of the Main Quills.

though in the case of Nos. 28 and 29 the cubital remiges IV. and V. were still somewhat short of their ultimate lengths.

B. *Remarks on the Period of Growth and the Development of the Remiges.*

Although the actual time required for the production of each quill itself cannot be followed with precision in the dead animal, neither is such the case with a bird in captivity, owing to altered conditions. But this can, nevertheless, be estimated tolerably well from a number of specimens which show a particular quill to be in moult within a given stage; and, further, with the aid of a quill just recently developed to full growth, as is the case in the majority of individuals showing more than one quill in successive stages of development at the time, and another one perhaps just emerging, when we get a valuable means for obtaining, by differential inference, an approximate result for the individual.

From the averages extracted for the period of growth for each quill, the result shows that those of the earlier stages develop faster than those of the later ones, which take somewhat longer to grow. The difference, however, is not considerable, and fluctuates between seven and ten days respectively. The range of time for the moult of the different remiges during a seasonal change can also be computed for the species as a whole, and a chart (Table II.), setting out the general result, having the additional advantage of showing their synchronic movements, has been appended also at the end of these remarks.

C. *The "Bastard Wing."* Alula *or* Ala spuria = Plumæ pollices.

In all robustly and normally developed individuals of this species I have never failed in finding the regular number of *pennæ*, which constitute this series, to be less than four. It is in weakly developed individuals only that their number is occasionally reduced to three. In such cases it is invariably at the expense of the innermost, or the first one if one regards them in the same light as the metacarpo-digital remiges.

Had there any additional proof been wanting on the remigial nature of these feathers, apart from a previous observation of the most proximal ones being sandwiched in between an abortive upper and a homologous ventral covert, nothing could have been more fortunate for dispelling the doubt as to their true value as flight-feathers than that shown by their moult.

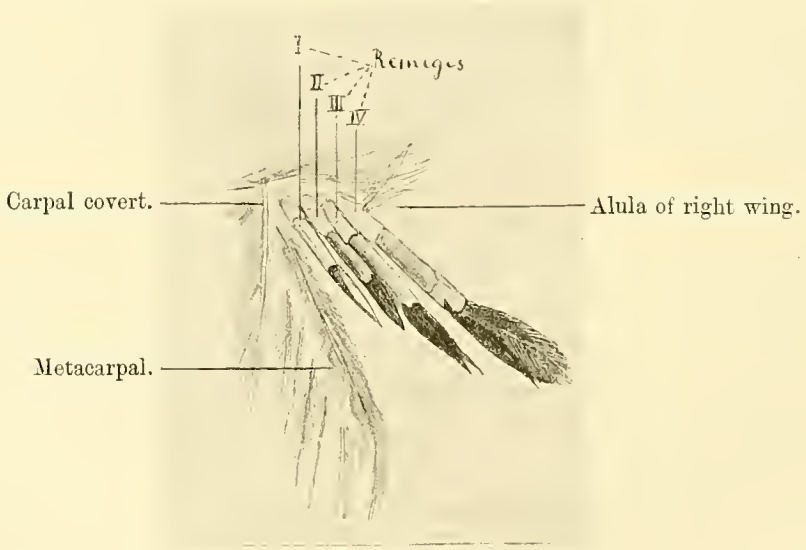
When I had received specimens representing the progressive stages of the moult for a consecutive number of weeks without having met as yet with any evidence on this point, I began to entertain serious misgivings of having missed what I then considered to be one of the most desirable points in this investigation.

As these feathers, it seems but reasonable to assume, are not greatly exposed to wear, it is at all times difficult, as I found, to distinguish between their old and their new growths, unless one secures the bird during their actual renewal.

It was a great satisfaction to me therefore when, on December 11th, I received the first specimen of a young female, numbered 14, which showed evidence of the moult for three out of the four feathers on both wings. A second bird, forming part of the same weekly complement, and which had received the serial number 13 on account of having been examined before the former, also a young female, exhibited no traces of moult for this part. This difference may be accounted for by the latter specimen being more backward in moult than No. 14 as regards one or two of the metacarpo-digital and one of the cubital remiges.

The next weekly instalment, consisting of four specimens, contributed nothing further to this stage of the moult. Curiously enough, another young female, No. 19 of the series, supplied the desired evidence for the whole of this set of feathers in such an excellent manner for both wings alike that nothing could be more perfect for a demonstration of the graduated succession of their growth, as seen in text-fig. 3, from my drawing of its right wing.

Text-fig. 3.



Showing the successive stages of development of the quills composing the Alula, from without inwards.

The figure shows the fourth longest and outermost feather, if not perfectly freed at its base from the *capsula*, to have at least acquired its ultimate full length. The next inner one, whose adhering capsule remains and encloses a greater amount of the new growth in proportion to the former, shows it to be about $\frac{3}{4}$ of its eventual length. The third innermost, being remex II., and the next in rotation of development, has attained one-half of its length; whilst remex I., or the innermost and last to appear,

has only reached the stage of development of a pin-feather, whose extreme barbs have just pierced the tip of its accompanying capsule. In text-fig. 3 these feathers are marked respectively, remiges IV., III., II., and I., in the order described above.

Another specimen received on the same date (January 16th) as the previous one, to which I have given the serial number 20, also shows the whole of this set in full process of moult on both sides of the wing, but is in a rather more advanced stage throughout.

Two specimens, Nos. 21 and 22, dating from January 29th, out of the total complement for that week, which also includes No. 23, also partake in this phase of the moult. No. 22 is slightly belated if compared with No. 20, whose early-accomplished *pennæ pollices* correspond with the moult of metacarpo-digital remiges V., VI., VII., and VIII. respectively; whilst in the case for the left side of No. 21, they correspond with primaries VI., VII., VIII., and IX. The right side is later still, where the 4th feather is the only one as yet replaced; this corresponds with metacarpo-digital remex VII.

Specimen 22, for an old female, presents a case of later appearance still, and, moreover, shows the additional anomaly of simultaneously producing (but symmetrically for both sides) the fourth and the second quills, whereby it has missed the renewal of the intervening third quill. The impending moult of this latter is indicated by its point just showing above the epidermis on the right side only, thus, as it were, rapidly remedying the deficiency. Seeing that this is the only specimen out of four quite normally moulting individuals, this case can be little else than the result of a faulty individual constitution.

In the remainder of the specimens received after this period, the moult of this series of feathers was invariably accomplished. It, moreover, shows that their moult is identical in period with that of certain primary remiges, and corresponds almost exactly with the extreme digital ones by slightly fluctuating between metacarpo-digitals VI. and X.

The relative position for the growth of these pennæ pollices to those primaries with which they moult in synchronism, based upon the highest aggregates received for each feather separately, will be found entered on Table VI., which is at the end of the technical description dealing with the feather-tracts in general.

The moult of these *pennæ* is of ever so much greater importance than their purely ordinal replacement when considered from the point of digital feathering as a whole. Whether the origin be a doubtfully remigial [1] or an admittedly tectrical one only is of no consequence in this place. At the most their metacarpo-digital value must remain undisputed, since the principal satellites, as will be seen, also reflect the ordinal

[1] The similar absence of sedentary neossoptiles on the tips of the first set of these feathers, the same as in the other remiges, ought, in my opinion, to be decisive on this point.

TABLE III.—Showing in Percentages the Deficiency in the Power of Flight during the various Stages, caused through the Perennial Moult of *Gymnorhyna tibicen*.

Date.	No. of specimen.	Sexes and Ages.	Left Wing.			Right Wing.			Grand Totals for both Wings.
			Metacarpo-digitals.	Cubitals.	Totals.	Cubitals.	Metacarpo-digitals.	Totals.	
1896. Nov. 5 ..	1	♂ ad.	14·6	1·3	7·9	3·4	17·5	10·4	9·1
,, ,, 5 ..	2	♂ juv.	13·6	2·2	7·9	1·6	10·0	5·8	6·8
,, ,, 14 ..	3	♀ juv.	15·7	12·3	14·0	9·2	13·4	11·3	12·6
,, ,, 14 ..	4	♂ juv.	21·3	12·8	17·0	11·0	23·2	17·1	17·0
,, ,, 14 ..	5	♀ juv.	10·6	17·6	14·1	8·9	10·8	9·8	11·9
,, ,, 19 ..	6	♂ juv.	13·5	7·3	10·9	8·1	14·0	11·0	10·9
,, ,, 19 ..	7	♂ ad.	6·9	18·5	12·7	6·6	7·5	7·0	9·8
,, ,, 19 ..	8	♂ juv.	3·1	1·3	2·2	·2	2·9	9·5	1·8
,, ,, 28 ..	9	♂ ad.	5·5	6·3	5·9	6·3	15·6	10·8	8·3
,, ,, 28 .	10	♂ ad.	12·0	35·7	23·8	20·4	12·4	16·4	20·1
,, Dec. 3 ..	11	♀ juv.	14·2	8·9	11·6	9·7	14·2	12·9	12·2
,, ,, 3	12	♀ juv.	4·0	22·9	13·0	17·5	4·4	10·9	11·9
,, ,, 11 ..	13	♀ juv.	4·9	14·3	9·6	15·5	12·9	14·2	11·9
,, ,, 11 ..	14	♀ juv.	24·2	13·0	18·6	21·9	14·2	18·0	18·3
,, ,, 19 ..	15	♂ juv.	16·6	17·7	17·1	9·0	13·2	11·1	14·1
,, ,, 19 ..	16	♂ juv.	5·8	14·2	10·0	20·8	6·0	13·4	11·7
1897. Jan. 1 ..	17	♂ ad.	13·6	16·0	14·8	20·8	9·4	15·1	14·9
,, ,, 1 ..	18	♂ ad.	10·2	13·0	11·5	17·0	8·4	12·7	12·1
,, ,, 16 ..	19	♀ juv.	8·2	10·0	9·1	12·5	4·3	8·4	8·7
,, ,, 16 ..	20	♂ ad.	8·9	7·1	8·0	7·3	8·3	7·8	7·4
,, ,, 29 ..	21	♂ ad.	13·0	·4	6·7	4·4	12·2	8·3	7·5
,, ,, 29 ..	22	♀ ad.	7·8	7·0	7·4	6·4	9·0	7·7	7·5
,, ,, 29 .	23	♀ juv.	16·5	13·1	14·8	9·1	16·2	12·6	13·7
,, Feb. 18 ..	24	♂ ad.	9·1	2·2	5·6	4·8	10·0	7·4	6·5
,, ,, 18 ..	25	♂ ad.	5·5	·5	3·0	·5	5·8	3·1	3·0 (5)
,, Mar. 4 ..	26	♂ ad.	2·1	9·6	5·8	9·2	6·4	7·8	6·8
,, ,, 4 ..	27	♂ ad.	4·9	4·0	4·4	1·0	5·8	3·4	3·9

For explanation of Table III. see p. 375.

sequence for renewal, as do the flight-feathers themselves, with the same constant accuracy of recurrence in the species. *As such, then, we have the astonishing fact standing, that they moult* (as may be seen from the drawing) *in an opposite direction to the metacarpo-digital remiges.* This is in no way an isolated occurrence, but a condition which one finds twice repeated on the cubitus, and which, as I believe I am justified in regarding, affords us the *key to the original*, if not *pentadactyle*, at least *tetradactyle feathering* of some ancestral type of birds.

D. *Extract from and Remarks on the Table of Percentages for the Deficiency in the Power of Flight.*

When consulting the foregoing Table (III.), it will be noticed that for both the lowest and the highest percentages the figures are distributed fairly equally without having any direct bearing upon either stage of moult, age, or sex of the individual. Thus we get minima and maxima at all times during the changes.

The *lowest* figures we get are as follows:—

	Metacarpo-digitals.	Cubitals.
Left side	2·1 (26)	·4 (21)
Right side	2·9 (8)	·2 (8)

Totals for left side.	Totals for right side.	Grand total.
2·2 (8)	3·1 (25)	3·0 (25)

The *highest* figures thus received are:—

	Metacarpo-digitals.	Cubitals.
Left side	24·2 (14)	22·9 (12)
Right side	23·2 (4)	20·8 (16 & 17)

Totals for left side.	Totals for right side.	Grand total.
23·8 (10)	17·1 (4)	20·1 (10)

(The figures within the brackets indicate the number of the specimen.)

It will be seen that, while the greatest amount of feather-loss incurred at any time during the moult occurs on the hand-portion of specimen No. 14 with 24·2 per cent., the cubital portion is only slightly behind this with 22·9 per cent., shown in specimen No. 12.

For the totals, the highest one obtained is in the case of the left-side wing with 23·8 per cent., as against one of only 17·1 on the other side.

An analysis for the different portions of the two wings, however, gives the general

result of an even balance for the specimens as a whole, as may be seen by the following figures :—

	Higher % losses.		Equal % loss.	Total.
	Left side.	Right side.		
Metacarpo-digitals	8 specimens.	10 specimens.	9 specimens.	27 specimens.
Cubitals	10 „	10 „	7 „	27 „
Composite wing	11 „	12 „	4 „	27 „

Perfect symmetry is present only in four specimens ; these are Nos. 4, 14, 22, and 25. For greatest differences of asymmetry amongst these specimens the numbers are distributed as follows :—

For the *metacarpo-digitals*, two out of ten specimens, namely, one each (for each side of the wing). These are Nos. 9 and 24.

For the *cubitals*, one out of 15 (for the left side). This is No. 10.

These differences get considerably levelled in their aggregates, as may be seen from the *totals* obtained between the left and the right wing of Nos. 8 and 10, which two specimens show the amount of this difference to be one of 7 per cent. for each.

Finally, as indicated in the column of percentages of the total feather-loss for both wings (see grand totals), this does not exceed $\frac{1}{5}$ of all the flight-feathers, as specimen No. 10 shows, with the highest total of all, viz. 20·1 per cent.

E. *The Wing-coverts.* Tectrices primæ serii *s.* majores.

1. *Superiores.*

The upper major coverts are usually the most prominent ones of the series which accompany the flight-feathers, and to which they are more closely related than are any of the remaining series. They also resemble flight-feathers entirely, both in texture and development. When fully developed, their length on the manus is about one-third part of each flight-feather in this species.

On the cubital portion these coverts are proportionately longer, covering about one-half of their respective remiges. But whilst the latter maintain a nearly uniform length as far as remex VII., from whence to the last or remex X. they rapidly decrease in length, their upper major coverts, on the contrary, slightly increase in length in the same direction, *i. e.* towards the upper arm.

In the flexion of the wing known as the carpal joint, the first covert belonging to the hand and the first one belonging to the cubital portion, which are directly approximated here, are of nearly equal lengths, as are also their respective flight-feathers.

Metacarpo-digital portion.—The order in which the dorsal major coverts make their appearance on the manus is precisely the same as that of the remiges, being one of perfect synchronism both for growth as well as for the respective sequence of renewal. I have never found any deviation from this principle in the normally developed

individuals which I have examined. Whenever I met with any exception it happened only where the remex in moult had been accidentally retarded in growth. The latter case can invariably be detected from the normal course of development which the major covert pursues, provided that the anomaly has not been caused by external injury.

Now and then the allied covert is shed a little in advance of its remex, but in the majority of individuals it is shed simultaneously with it. Only in three cases did I find the conditions reversed—that is, the remex preceding the principal dorsal covert in moult by being shed first.

The rule therefore of the dorsal major coverts slightly preceding in moult their respectively accompanying flight-feathers is a character inherent to the conditions prevailing for the acquisition of the first or plumage of the fledgling bird.

This law being so uniformly carried out as regards the metacarpo-digital portion, a few remarks, having reference to the alleged *undecem-pennate* forms of Passerine birds of Gadow (21), may be made here.

So long as it was taken for granted generally that the main covert directly associated with a quill was the one which lies proximad to the latter, it follows that Dr. Gadow was without question fully entitled to the conclusions he had then arrived at in regard to the exact relationship of the terminal feathers. But, when inquiring later into this matter (Degen (16), pp. x–xiii), I was able to show histologically, as well as by means of the physiological conditions of moult (see also figures 2 & 3, *l. c.*), that the conditions were invariably reversed, viz., that the major coverts most intimately connected with the main quills were those which are lying *distad* to the latter. This naturally had the effect of leaving one feather less to be disposed of, instead of the two supernumerary ones as in the case of Dr. Gadow (his alleged 11th quill and its corresponding covert), for a great number of genera and species of *Passeres*; those with 9 and those with 10 primaries alike, including amongst the latter also the species under special consideration. Dr. Gadow's own words (pp. 659 & 660, *l. c.*) on this point are:—"In some cases there might be some doubt whether the little terminal feather in question is really a primary, but this can easily be settled by the presence of the corresponding upper coverts. Moreover, *there are many cases in which the primary is still longer than its covert* [1]. When the 10th or 11th quill is much shortened, *the corresponding lower covert is absent in the Passeres* [1]. The *Alaudidæ* prove that the 10th quill is capable of being shifted dorsalwards, so that it becomes enclosed between the outer vane of the 9th primary and the 10th upper covert, instead of being freely visible below and in front of the 9th primary; when seen from below, it is hidden by the outer vane of the 9th primary. This shifting explains the conditions which are the rule amongst the birds of Group D (p. 664, *l. c.*). *The 11th primary undergoes a similar dislocation in a more marked degree*" [1].

[1] These *italics* are mine.

In agreement, then, with the issue of flight-feathers on the hand-portion of the wing, if the terminal feather in question were a primary, it follows that, like the remainder, it should moult in turn, after the renewal of remex X. Such, however, is not the case, as specimen No. 24—the only one showing this stage—proves. On the right wing of the latter this feather has been renewed, whilst remex X. is still the old one, and its own major covert, recently shed, lying distad to it as previously explained, is just emerging, showing the apex of the new growth, anticipatory of the shedding of remex X. itself. This particular stage of moult is slightly in arrear on the left-side wing of this specimen, the general conditions being otherwise quite similar. Here, however, instead of this alleged primary being renewed already (it proved to be the old one yet by accidentally dropping out upon being touched, which is a sure sign of its impending renewal) before the covert belonging to primary X., the old one was not yet shed. There is consequently a strong probability in favour of this terminal feather being the major covert belonging to the ventral series (median ?) of the suppressed remex XI. (*remicle*), by its moulting in advance of the remiges, a condition which does apply to the ventral series, as we shall see further on when considering their moult.

Cubital Portion.—The conditions under which these major coverts issue differ so widely from those previously dealt with that they are well deserving of more careful consideration.

Whilst there is the same unalterable mode of renewal retained for this series of feathers on the manus throughout all subsequent periods of general moult by repeating the first mode of acquisition, such is not the case for the major coverts of the cubital portion.

Here we are confronted by the occurrence of several transitory stages between birds of the first season and those of subsequent ages. Broadly speaking, there are three different stages conspicuous [1], which may be further subdivided as follows :—

Stage I. Condition of renewal for Bird of second season.

(*a*) Growth of major coverts (0) 1–7 simultaneous (0 representing carpal covert).

(*b*) Growth of coverts 8–10 consecutive in the order of these numerals forming Group 1.

Following upon the mode of the renewal of the first season's bird or fledgling stage, which consisted of the simultaneous growth of the whole series of these coverts from 1–10, the mode of the first perennial moult differs by coverts 8, 9, 10 constituting themselves into a definite group. Specimen No. 4 represents this first stage in a striking manner on both wings (*cf.* fig. 1, Table IV.). The major coverts 8–10 are differentiated from those of 1–7, which are all of uniform length in development, by

[1] This refers to renewal only, and does not include the initial stage of feathering of the fledgling.

being graduated in length of growth, a condition which corresponds with that of their corresponding flight-feathers. This first grouping arrangement is well defined in all the specimens of birds of the second season and upwards.

Stage II. Group-moulting of various degrees of development.

1. Consisting of formation of previous Group (I.) with the remainder of coverts (0–7) renewing from 7–1 (0) in outward direction. (See Table IV. fig. 1.)
2. Consists of coverts (0) 1–4, or Group II., renewing in an inward direction. All the feathers of this second group are either equal in length or partly in graduated condition of development. In the latter case they are supplied from without inwards. (See Table IV. fig. 2.)
3. Consists of coverts 5–7, forming Group III. The feathers belonging to this third group at this stage appear still simultaneously (*cf.* diagr. Table IV. fig. 3). (Feathers in nascent condition of development.)

The first degree is common to all individuals, both young and old, and particularly clearly defined for Group I. in specimen No. 4, as quoted already. (Table IV. fig. 1.)

The second degree is represented by specimen No. 2, more particularly so for the right wing; by No. 6, left side; and No. 14 on both sides. (*Cf.* Table IV. figs. 2, 3.)

The third degree of this stage of moult, represented in diagram by specimen No. 19 (see Table IV. fig. 3), occurs on right side of specimen No. 5, both sides of Nos. 9 and 15, and on the right-side wing of No. 23. In the latter specimen we have a remarkable combination of two cases of transition from one stage to another by its left-side wing already adopting the more advanced condition of the fully adult individuals of the last, or

Stage III. In which the main dorsal coverts follow the same perfected group-arrangement of moulting in synchronism and in the identical order of appearance as their respective remiges. This condition is shown in the diagrams by specimen No. 24. (See Table IV. fig. 4.)

This last stage is achieved only by the oldest individuals, and is attained by the metamorphic steps of consecutive moults, commencing with the young and finishing with the fully matured bird.

Further examples of this latter kind are to be seen on the left side of No. 21, an adult male, in which the carpals and coverts 1 and 2 have been completed, as have their respective remiges. Coverts 3 and 4 are equally incomplete as are these remiges. This condition obtains independently and in addition to the renewal of coverts 8–10 as a first definite group. On the left side of No. 23, a young female, we have, besides the same independent final formation of Group I., the incomplete growth of coverts 3 and 4, which, though slightly in advance of growth as compared with the other side, is proportionate to that of their equally incomplete remiges; whilst at this stage,

covert 7, which is in a nascent condition of growth, foreshadows the impending moult of the remex with which it is associated. Coverts 5 and 6 appear to be the old feathers as yet unaffected by moult.

There is no necessity to dwell in detail upon all the remaining old individuals, as they obey the law stated in the cases quoted above, which is that of perfected group-moulting as it applies to the flight-feathers which occupy the cubital portion of the wing.

Unlike the well-defined synchronism with which the upper major coverts keep pace with the remiges of the hand-portion, there exists a marked contrast in the way they make their appearance on the forearm, inasmuch as they follow the general tendency for moulting in advance of their allied remiges, irrespective of age. Through some inexplicable agency, and for a much longer period—in fact, through nearly every moult during the bird's life,—they adhere to the more primitive conditions of the first, or fledgling livery. The only admissible inference to be drawn from this fact must be one largely in favour of this early endowment of wing-feathers to be a secondary provision and of ontogenetic origin.

2. *Inferiores.*

Metacarpo-digital Portion.—The difficulties in following up the order of renewal which this series adopts are greater than those attending the researches into the previously considered upper series. The chief one arises from the circumstance of the more protected position which they occupy on the inner side of the wing, and in which they suffer less from the effects of wear than feathers which are constantly exposed. Hence the greater difficulty for determining between old and new growth in fully developed feathers. It is only when particles of the capsule within which they were formed are still adhering to the recently renewed feather that the fact can be ascertained, or where the renewal consists of feathers in a state of nascent growth. We cannot expect to meet with the latter phase in any considerable number of individuals alike, and therefore I could find positive evidence on this head only in 9 birds out of 25 specimens after deducting Nos. 26–32, which are in a state of actually complete renewal or nearly so.

With one exception only, viz., that of the old female No. 22, these specimens are characterized by almost perfect bilateralism of symmetry on the two wings as regards the hand-portion for the moult of this series of coverts. These are Nos. 1, 14, 16, 17, 18, 19, 20, 22, 24, and 25. According to their ages and sexes they range as follows:—

		Totals.
Males.	Old: Nos. 1, 17, 18, 20, 24, 25	6
„	Young: No. 16	1
Females.	Old: No. 22	1
„	Young: Nos. 14, 19	2

By leaving out from immediate consideration the old male No. 1, obtained in the

first batch of Nov. 5, with Nos. 2 and 3, it is noticeable that, of the birds received before the dates of December 11 and 19, which are represented by specimens Nos. 14 and 16 respectively, none exhibit any signs of moult having set in for this row of coverts. Nearly all of these represent young birds, and there is good reason for assuming that Nos. 9 and 10 are not fully adult either, as I considered them to be at that time, judging from external appearance alone. It is therefore evident that the renewal of this row amongst younger birds does not set in until about towards the middle of the period of perennial moult.

The renewal of this series takes place in the same order as that of their respective remiges and upper major coverts, which commences with the innermost and concludes with the 10th or outermost, though differing in regard to chronicism according to age.

In the youngest birds no lower major covert is renewed until nearly six to eight flight-feathers have been formed. From this retarded appearance every subsequent moult recovers one or two places from the flight-feathers which moult in advance of them, till, finally, in the perfectly adult stage, their renewal synchronizes absolutely with that of the flight-feather with which they are associated.

The most instructive specimen on the list, representing this culminating phase, is that of the old male No. 1 (see Table IV. fig. 6), which is also one of the earliest for beginning the moult for this series of feathers. Its remiges I. and II., together with their dorsal major coverts, which under all circumstances are the earliest to moult, are simultaneously accompanied in moult by their respective ventral major coverts. Indeed, on its left side, the inferior covert 3 is slightly in advance for making its appearance of the old remex III., which, having just been shed off, shows no sign yet of the new-growth quill. The same condition obtains for the remiges on the right side of the wing, the inferior coverts 1 and 2 being synchronous with the dorsal ones, which are being renewed also at this stage.

The adult male No. 25 is similarly characteristic for almost perfect synchronism, though No. 24, an old male too, of which a diagram has been appended (Table IV. fig. 4), represents one of the later stages of transition from the juvenile to the fully adult phase of this row in relation to the flight-feathers. Both these specimens were procured towards the end of the moulting-season, as their numbering shows, and accordingly were in a much more advanced condition of the moult.

The remaining specimens, Nos. 17–20, represent every conceivable transitory phase of retardation from their remiges by a steady progression for each moult of one ventral major covert, from their original arrear of 8 (well instanced by specimen No. 18, see diagr. Table IV. fig. 5) down to the case of absolutely simultaneous movement so characteristic of adult birds, as explained above; this is continued through every subsequent moult of the bird's life.

The diagrams on Table IV. (major coverts) for specimens Nos. 18 (fig. 5), 14 (fig. 2), 19 (fig. 3), 1 (fig. 6), and 24 (fig. 4) illustrate some of these transitory stages.

Cubital Portion.—This row of covert-feathers being suppressed in all the Passerine birds, no positive information is available through this species for their behaviour under conditions of moult.

A provisional examination of a *diastataxic* species (*Platycercus eximius*) shows that there is no material deviation from the moult of their dorsal congeners as regards synchronism with their remiges, excepting perhaps that they exhibit a tendency to moult somewhat earlier than the latter and also adhere to the juvenile mode of simultaneous replacement through more than one perennial change.

Tectrices secundæ serii *or* Tectrices mediæ.

1. *Superiores.*

Metacarpo-digital Portion.—In striking contrast to the order of the moult which is adopted by the first series of satellites in relation to the remiges, stands that of the second series, or the medians.

In the former, as we have seen, it consisted in a rhythmical accompaniment to their remiges in the order of the growth of the latter. Not so for the dorsal median coverts. *Their renewal proceeds from two separate points on this portion of the wing.*

The first of these two points, the earlier one at which moult sets in, is identical with remex I. and its upper major covert. Its moult, however, does not synchronize with these, because the earliest signs of moult of median coverts do not appear until after the renewal of from 4–5 remiges with their principal satellites has taken place.

The second point at which moult sets in on the manus coincides with remex VII., and proceeds in the same outward direction as does that from the proximal centre.

This different mode of renewal therefore bisects the hand-portion into two areas: a first or proximal one comprising median coverts 1–6, and a second or distad section made up by coverts 7–10. In birds at the beginning of the moult, and in which not more than from 2–4 remiges are in process of renewal, as yet no medians make their appearance.

The earliest specimen on the list in which the first and innermost of median coverts is being formed is No. 3 on its right-side wing, which has reached the stage of *e* (see also Diagr. B, Plate XXXVI., right side), or the moult of remex V. The next specimen is No. 6, on the right side, too, of which median coverts 1 and 2 are in course of formation. Its stage of development for remiges is the same as that of the previous specimen, viz. that of remex V., which denotes a slightly more advanced condition here. This specimen, moreover, has reached a more advanced condition on its left side, where median covert 3 is being renewed also. The renewal of 3 median coverts, however, generally coincides with that of remex VI., which is the more normal course which these coverts pursue. This is well defined on the right side of No. 9.

[*To face* p. 382.

EXPLANATION OF TABLE IV.

The letters **M.C.D.** or **C.**, placed above each diagram, signify *Metacarpo-digitals* or *Cubitals*.

The Roman cyphers, from I. to X., above the symbols ○ ○ &c. of figure 1, denote the numerical order of the remiges and the major coverts, with which they are allied, and apply also to the other diagrams beneath.

The darts placed over or below any sub-series of major coverts point in the direction of their respective sequence of moult.

The spherical symbols (and further explained on table itself) represent a theoretical cross-section through the projected quills and coverts for which they stand, made longitudinally the whole length of the posterior margin of the extended wing, or portion of it, as in the case of figs. 5 & 6.

Fig. 1. Showing Group-moulting for the upper major coverts VIII.–X. on the cubitus, and the simultaneous appearance for I.–VII. in relation to their remiges under moult (Degree 1). Also showing the relative movement of the remiges and the major coverts for the hand-portion.

Fig. 2. Shows upper cubital major coverts I.–IV. inclusive of carpal covert, forming Group II. by moulting in an inward direction, or one opposed to the stage for the same sub-series, illustrated in specimen represented by fig. 1. It further shows the first stage of moult in relationship to the remiges of the inferior major coverts for the hand-portion (2nd degree).

Fig. 3. Shows the 3rd degree, or that of cubital major coverts V.–VII., constituting Group III., its integers as yet appearing simultaneously. It also shows the more advanced condition of moult for the progressive movement of the ventral major coverts on the hand-portion of the wing.

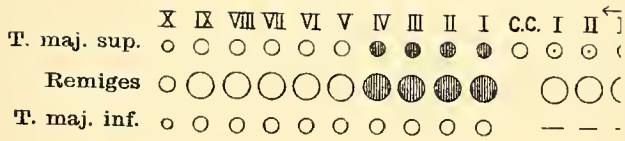
Fig. 4. Shows the final stage of moult in their relationship to each other of the remiges and the major coverts, both upper and lower, in synchronous Group-arrangement for the cubitus, and in regular sequence outwards for the metacarpo-digital portion, a mode which is adopted only by the fully adult bird.

Fig. 5. Shows the initial stage in the replacement of the inferior major coverts for the hand-portion.

Fig. 6. Represents a similar stage, though slightly in advance of that seen in fig. 5.

Stage I

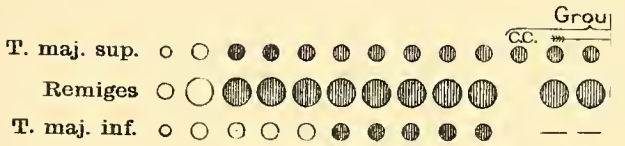
M.C.D.



Stage II

M.C.D.

M.C.D.



Stage III

M.C.D.

E. Degen, del.

Diagr

TABLE IV.

To face p. 382.

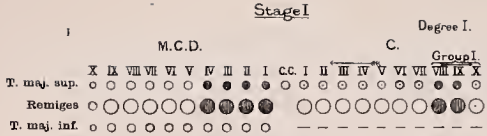


Fig. 1.

Spec. No. 4. juv. ♂

Fig. 5.

Spec. No. 18. juv. ♂

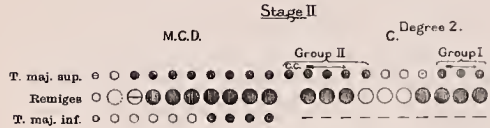


Fig. 2.

Spec. No. 14. juv. ♀

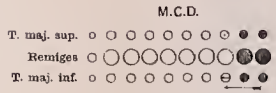


Fig. 6.

Spec. No. 1. ad. ♂

Fig. 3.

Spec. No. 19. juv. ♀

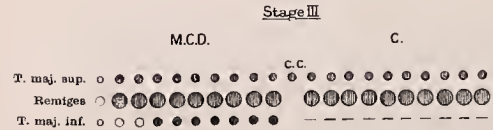


Fig. 4.

Spec. No. 24. ad. ♂

EXPLANATION OF THE SYMBOLS USED IN TABLES IV & V.

Old quills and coverts	thus	○ ○
New growth of quills and coverts	"	● ●
Shed off " " " "	"	◌ ◌
Part grown " " " "	"	⊖ ⊖
Nascent " " " "	"	⊙ ⊙
Absent row " " " "	"	— —
Coverts not under consideration	"	+ +
Carpal coverts	"	C. C.

E. Degen, del.

Bale & Danielsson, Ltd.

Diagrams illustrating the movement under conditions of Moult of both the Dorsal and the Ventral Major Coverts.

The renewal of median covert 4, which is the next stage, as a rule corresponds with that of remiges VI. and VII. To this condition, specimens Nos. 7 (right side), 10 (both sides), 11 (both sides), and also 15 testify very clearly.

At this stage the 5th median covert is frequently shed also, preparatory for its speedy replacement, though in the majority of cases its moult corresponds with that of primary VII., as does also median covert 6, whose moult rapidly follows that of the 5th of this series.

The morphological features for the coverts of the outer section, or distad area, are as follows:—Dorsal median-covert 7 is renewed when the synonymous coverts 2 and 3 of the inner section are formed—that is to say, in advance by one place of remiges V. and VI. under moult (see diagr. Table V. fig. 1, referring to right side of specimen No. 5). Synchronous with the formation of medians 1–4, the 8th also follows on in rapid succession to the 7th. This is well marked in specimens Nos. 7 (Table V. fig. 2 of diagr.) and 10 (both on right side). At the time of the formation of medians 5 and 6, the last two to moult of the proximal area, the 9th and the 10th or last coverts of the distal area are also developed in rapid succession of each other. This phase corresponds with that constituting the renewal of remex VIII.

In this manner, then, the moult of the medians forming the outer section is invariably accomplished considerably in advance of their corresponding remiges VIII., IX., and X. This is particularly noticeable in those specimens which partake of the later stages of the perennial moult. These are Nos. 15–24, but especially is this the case in No. 11 with its 5th covert just shed, and which, by still retaining the old covert 6 on the right, also shows coverts 7, 8, 9, and 10 in a state of complete renewal. This typical case for the relative position of the moult of these coverts is seen in the diagrams of Table V. specimen No. 7 (fig. 2) and No. 11 (fig. 3).

In birds of the season, however, the mode of renewal for the feathers of this series is a simultaneous one still, the same as it is for the fledgling. This is seen in Nos. 2, 12, and 14—birds which are undergoing their first autumn moult in the season in which they were hatched. Specimen No. 12 in Table V. fig. 4 shows this particular condition.

Cubital Portion.—The median coverts of this portion of the wing evince a strong tendency not only for keeping pace with the moult of their respective remiges, but actually preceding them, though not to such an extent as in the case of the major coverts, of which latter they are, therefore, in arrear. This is not only noticeable in the case of the young individuals to which the embryonic condition for simultaneous moulting applies, analogous to that of the major coverts, but a similarly accelerated appearance of this series is seen to take place when the series is broken up, in order to moult in groups, which is the ultimate adoption of renewal in the mature bird. The transition from the former to the latter is effected by various intermediary stages, which lead up to the same grouping-system as that of the remiges, viz. their subsequent alternate direction of moult.

In the majority of the specimens the growth of these coverts proceeds in a fairly symmetrical manner from both wings for either of the two systems of moult. It, however, happens frequently, notably in the younger birds, that while the juvenile mode is prevailing still on the one wing, the other wing may have already adopted a stage of the later conditions.

Instances of perfect symmetry for the earlier stage of simultaneous development of the series are Nos. 5, 12, and 15, which are all young birds; while a case of dualism of development occurs, amongst others, in No. 13. In this latter specimen the wing of the left-side is still following the early principle of simultaneous replacement; it is marked in this case by uniformity in length of all its coverts which constitute this co-series; whereas on the right side, while still repeating the early mode on the proximal portion of the cubitus from the 5th covert to the 10th (including a slight modification of the 8th), the mode of the first definite formation for moulting in groups has taken place on its distal part for coverts 1–4. This is shown by the diminishing lengths in development of these coverts in their inward numerical order.

In reference to the modification of covert 8, as alluded to above, it is not a little curious to find this covert to be the only one in a nascent state of growth amongst those from 6–10, which are all about half-grown. Herein, then, we have an early indication of plainly denoting the initial point in the ultimate formation of the first group, which comprises coverts 8, 9, and 10. This arrangement corresponds exactly with that of the issue of the remiges and the main coverts in this place which have preceded them in development.

Illustrations of perfect conditions for the group-moulting are Nos. 3 (left side), 11 (both sides), 13 (right side), 16 (right side), and probably all the remainder of adults in which the moult of this co-series had been positively completed at the time of their reception.

2. *Inferiores.*

Metacarpo-digital Portion.—Quite distinct from the mode of renewal by means of two separate sections of their dorsal congeners at a comparatively immature age, the set of coverts under consideration here *apparently* follows the rule which applies to the remiges and the main coverts of the young individual undergoing its first autumn moult, viz. in the ordinal appearance of the feathers from 1–10.

The main cause for this *apparent*[1] difference lies in the fact that they begin to moult later than their companion coverts of the dorsal series; but this is a delusion only. It is not until from three to four of the latter have emerged and are fairly developed that the first ventral median begins to replace its old feather. The others follow suit in rapid succession, completing the inner section with the 6th, and so reach the 7th covert or first of the outer section at about the same time as this latter emerges from the skin. This arrangement gives it the appearance of a continuous growth for the whole series, and *therefore produces* the *delusion* referred to before.

Fortunately, among the specimens procured to supply data for the various stages, No. 15 provides us with the desired information on the subject, where *medeæ inferiores* 1, 2, and 3 of the inner area, and 7, 8, 9, and 10, belonging to the outer one, are in course of renewal. That it is not a merely accidental circumstance, but a reliable case, is further evidenced by the perfect symmetry of the occurrence on both wings.

The relative position for the renewal of the ventral series in the juv. ♂, specimen 15, to their dorsal congeners (see diagram of Table V. fig. 5) can be adequately formulated thus:—

Metacarpo-digital Portion.

	Left wing.		Right wing.	
	Distal area.	Proximal area.	Proximal area.	Distal area.
Dorsal series . . .	10, 9, 8, 7, ——	4, 3, 2, 1	1, 2, 3, (4)°, (5)°, —	7, 8, 9, 10
Ventral series . . .	10, 9, 8, 7, ———	3, 2, 1	1, 2, 3, ————	7, 8, 9, 10

The symbol o, placed above figures 4 and 5 of the coverts of the dorsal series of the right side, denotes that these feathers were recently shed, thus showing the relative movement for the different constituents of this row to be in nearly perfect synchronism within the two areas; whereas for the left wing the 4th covert of the dorsal row, having been replaced already, constitutes a case of retardation for the proximal area, the old covert 5 being still retained.

However, individuals older by a season or two acquire perfect conditions of synchronism for the dorsal and ventral rows within the same area, and a highly instructive example of this is seen in the old male No. 10 (see also Table V. fig. 6), which, moreover, shows the connection of the moult between the inner and the outer area for the *ventral* medians, as below:—

Metacarpo-digital Portion.

	Left wing.		Right wing.	
	Distal area.	Proximal area.	Proximal area.	Distal area.
Dorsal series . . .	—— 9, 8, 7, ——	(4)°, 3, 2, 1	1, 2, 3, 4, ———	7, 8, ——
Ventral series . . .	———	(8)°, 7, (6)°, 5, 4, 3, 2, 1	1, 2, 3, 4, 5, ——	7, 8, ——

It may be seen from the above formula that there is a slight overbalance of synchronism in favour of the first division for the *ventrals* in the shape of covert 5 on the right side, and, in addition to this covert 5, on the left by the 6th covert being shed preparatory to its immediate renewal. This sectional synchronism can be studied only on those few specimens which represent individuals of middle age, combining with the latter requisite that also of this particular phase of the perennial moult. In the specimens procured at a later period, the moult of this series is invariably completed throughout.

During the first total feather-change in the young bird, and to a great extent also in that of the following season, all the feathers constituting this series make their appearance simultaneously and parallel with the dorsal row of medians 1–10, without the ultimate division into the metacarpal and the digital area, which is so characteristic for subsequent moults. In this case, however, the synchronous development with their equivalents of the dorsal series is a perfect one in their entirety. Partly in the second, but wholly so in the third season, the transitory step from the one mode to the other is effected by an intermediary stage. This consists in the inferior row moulting in arrear of the dorsal one still, while yet adhering to the non-deciduous form of renewal by means of a gradual supply of the feathers which begins with covert 1 (the innermost) and ends with 10 (the outermost). The dorsal row has meanwhile already acquired, either on one side only or symmetrically from both wings, the perennial or deciduous style above mentioned of the areal form of moult.

Nos. 7, 8, 11, 12 (see also diagrams for these, Table V. figs. 3 & 4), and also 13 are examples of specimens of either one or the other of these transitory cases. The fully adult mode of moult, in which the ventral equivalents are renewed in absolute synchronism with the dorsals, is reached only when the bird attains the positively adult stage, and not before the 4th annual moult.

An approximate key to the various phases of the relative development between the dorsal and ventral rows is appended at the close of the description for the whole of these series (see p. 390).

Cubital Portion.—Bilateral symmetry, as we have seen it to exist mainly for the hand-portion of the wing, is not nearly so pronounced a feature on the forearm for this row of feathers. Out of 10 specimens showing this phase of the moult there are 3 which show cases of asymmetry in the corresponding portions of the two wings, as the following analysis of these specimens shows:—

Symmetrical Development.

Males.	Old: Nos. 17, 20, 24, 25	4	
„	Young	—	
Females.	Old	—	
„	Young: Nos. 14, 19, 23	3	
	Total . .	—	7

Asymmetrical Development.

Males.	Old: No. 1	1	
„	Young: No. 4	1	
Females.	Old	—	
„	Young: No. 12	1	
	Total . .	—	3
	Grand total		10

EXPLANATION OF TABLE V.

T. med. sup. = Tectrices mediæ superiores.

T. med. inf. = Tectrices mediæ inferiores.

Cyphers, symbols, and other abbreviations similar to those used in Table IV.

Fig. 1. Metacarpo-digital portion of right-side wing, showing the moult of medians I. and II., and the first to appear of the proximal section. Also median VII., the first covert of the distal section.

No inferior medians in moult at this stage.

Fig. 2. Metacarpo-digital portion of right-side wing, showing the more advanced condition of four medians belonging to the proximal section in moult, and two, medians VII. and VIII., on distal section.

Inferior medians I., II., and III. in moult also at this stage.

Fig. 3. Metacarpo-digital portion of right-side wing, showing dorsal median V. of proximal section as the next in turn, shed off, preparatory for its replacement by new feather.

All the coverts of this series belonging to the outer section are replaced, also the whole series of the ventral or inferior medians.

Fig. 4. Metacarpo-digital portion of right-side wing, showing the renewal of the dorsal medians in regular sequence of their ordinal numbers, irrespective of the two sections, and a typical instance of the perennial moult of a first season's bird.

Fig. 5. Metacarpo-digital portion of left- and right-side wing.

In this the sub-serial renewal for the two sections may be seen; both for their chronicism between the dorsal and the ventral series of medians, as it takes place in a younger individual.

Fig. 6. Left- and right-side metacarpo-digital portions of the wing, also showing the chronological renewal of these series in the case of the fully adult individual.

Fig. 7. Cubital portion of the right-side wing.

Principally shows the mode of renewal for the inferior medians in the very young bird in their consecutive order for the whole series towards the wrist-joint from X.–I.

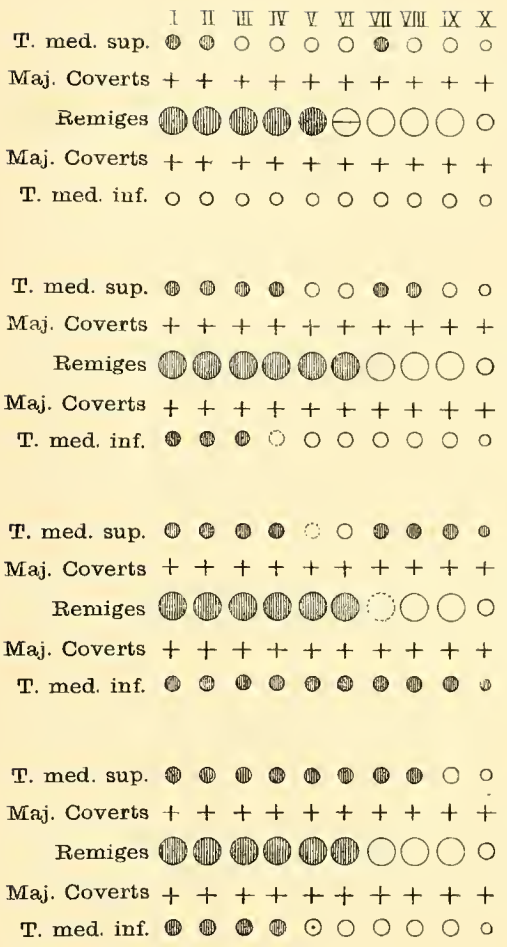
Fig. 8. Cubital portion of right-side wing, by specimen showing the typical condition of the moult of the dorsal medians in advance of the remiges.

Also showing first signs of Group-moulting for the inferior row, in which coverts I. and II. belonging to Group II. moult in opposite or inward direction.

Fig. 9. Cubital portion of right-side wing, showing more advanced condition of previous diagram by 4 inferior medians being in progressive stages of growth, also in inward direction of moult; while those of group I., or medians X., IX., & VIII., are as yet adhering to the conditions of the moult of the fledgling bird, *i. e.* by moulting in an outward direction.

Fig. 10. Cubital portion of the left wing.

This is an example of the final phase in the replacement of the inferior median coverts, and shows the ultimate grouping-arrangement with directions of moult—inwards for Groups I. & II., outwards for the middle or Group III.



Various phases from the Moult of the M
Coverts on Metacarpo-Digital Portion of

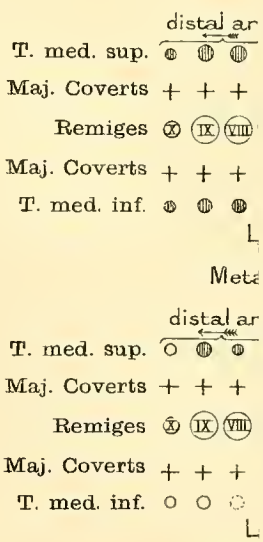


Fig. 5.

Fig. 6.

E. Degen, del.

Diagrams explaining
Median Coverts f

TABLE V.

To face p. 386.

Fig. 1.

Right Side Wing of Spec. No. 5 juv.♀

Fig. 2.

Right Side Wing of Spec. No. 7. juv. ♂

Fig. 3.

Right Side Wing of Spec. No. 11. juv.♀

Fig. 4.

Right Side Wing of Spec. No. 12. juv.♀

Various phases from the Moult of the Median Coverts on Metacarpo-Digital Portion of Wing.

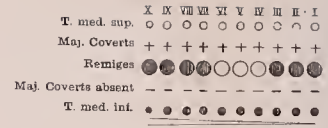


Fig. 7.

Spec. No. 14. juv. ♀ Right Side Wing.

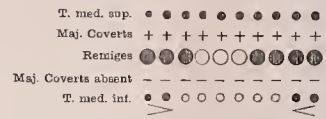


Fig. 8.

Spec. No. 17. ad.♂ Right Side Wing.

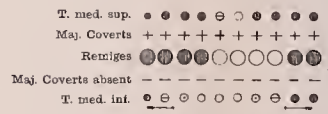


Fig. 9.

Spec. No. 11. juv.♀ Right Side Wing.

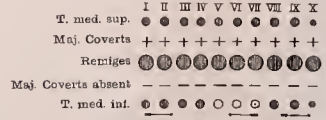


Fig. 10.

Spec. No. 24. ad. ♂ Left Side Wing.

Various phases for the Moult of the Median Coverts on the Cubital Portion of the Wing.

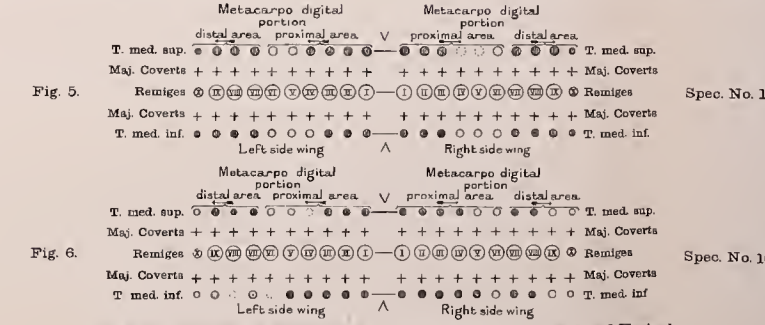


Fig. 5.

Spec. No. 15. juv.♂

Fig. 6.

Spec. No. 10. ad.♂

E. Degen del.

Bale & Danielsson, Ltd.

Diagrame explaining Relationship of Growth between the Dorsal and Ventral Median Coverts for the two Hand Portions of the Left and Right Wing.

The moult of these inferior medians, moreover, appears to be more erratic than is the case for the corresponding dorsal row of coverts. Besides this there exists a strong tendency to adhere to the conditions of the first endowment, in which the whole series is provided by a gradual advance of the growth from the elbow- towards the wrist-joint. The young female, No. 14 (see diagram Table V. fig. 7), is a particularly typical case of such a repetition of conditions, and so also is No. 4, a younger female still, as regards its left side only.

It is not, therefore, until the more matured specimens are consulted that the same plan as the one ascribed to their dorsal companion-coverts will be found to have been resorted to, namely, the moulting of the feathers within the groups in distinctly alternate directions. Even this, their ultimate order of perfect synchronism of movement with their respective remiges and major coverts, is not achieved by any but positively old birds, and that tendency to retardation, as referred to above, prevails for a considerably longer period of the bird's lifetime. The diagrams for the specimens of Table V. figs. 7–10 further supplement the explanation given above for the relative position of the ventral to the dorsal median coverts.

This conservative tendency is fully borne out by specimen No. 17 (Table V. fig. 8), which, although being entitled in other respects to be put down as an old male, has, nevertheless, only four of these coverts renewed in proportion to the eight cubital remiges on both wings; these are inner coverts 9 and 10, and the outer coverts 1 and 2. No. 20, too, with the same number of remiges renewed already as No. 17 (the previous specimen), has only two of these coverts in moult.

This tenacity to adhere to the juvenile conditions of growth is carried far within the grouping arrangement also in No. 11 (Table V. fig. 9), in which it is adhered to in the first group, comprising coverts 8–10, whose numbers instead of being renewed in this, their ultimate numerical order, are being still renewed in inverse order—that is, from 10 to 8, as they would be in a bird of the first season's plumage. On the other hand, this same individual shows for coverts 1, 2, 3, and 4 (inclusive of the carpal covert), which form the members of group 2, all the conditions followed by a bird of a more advanced stage, by beginning the moult from the carpal joint to the 4th, *i. e.* from the wrist towards the middle. The old males, Nos. 24 (see also diagr., Table V. fig. 10) and 25, approach the conditions of perfect synchronous development with their flight-feathers; and, further, the old male No. 1 equally bears reliable testimony on its left side for inferior median covert 8 being the first to be renewed, together with its corresponding main quill.

In addition to the remarks made above on the subject of bilateral symmetry, it should be pointed out that not only are cases of asymmetry more numerous when compared with the corresponding two cubital portions of the wing, but also for their hand-portions. Thus, in old males three out of a total of eleven are asymmetrical;

young males one of two; also the single old female which represents the moult of this series is asymmetrical for the metacarpo-digital portion; and of the four young females three are similarly affected.

Tectrices tertiæ serii *s.* minores.

1. *Superiores.*

Although this series of coverts is of minor importance to the flight-power of the wing, the manner in which they moult is of some morphological consequence.

Metacarpo-digital Portion.—On the manus the dorsal coverts of this series frequently precede in moult the other satellites. This they generally do in the same order as those of the higher series. But, as happens sometimes in the case of their cubital equivalents, several of them make their appearance simultaneously. They are unimportant for the covering of this part and of abortive growth.

Cubital Portion.—Here these coverts are confined to a single row also. The typical manner in which they are renewed imparts to them a special morphological feature, which is of some value as regards the definition of the different series.

Their moult differs markedly from their neighbouring rows of "marginal coverts" on the patagium and of the true covert-feathers whose description has already been given.

Their moult consists in a successive supply which begins with the innermost—contemporaneously almost with that of the feathers constituting the "parapterum," which latter in its turn follows that of the "humeral tract,"—and ends with the outermost. The coverts of this series do not take part in the grouping arrangement which is so characteristic a feature in the major coverts and the medians—not even in the fully adult.

The tendency for simultaneous development of three and four feathers is very prominent, and prevails more or less in every perennial moult. Whenever such is the case, it invariably takes place from within outwards, viz. the 10th to the 1st.

Furthermore, this mode of renewal distinguishes the row from the marginal series, whose renewal, although following the same outward direction generally, takes place in patches which begin on the anterior edge of the patagium, whence it spreads over both the dorsal and the ventral side of the wing in such a way that the several longitudinal rows are diagonally affected at the same time.

Thus it is through the agency of the moult principally that their morphological character as a row of covert-feathers can be equally established as being derived from a different source than either the higher series or the marginals. Where, as for instance in the more primitive forms of birds, the minors consist of several rows, these are generally made conspicuous by reversed overlap, a feature which has so greatly engaged the attention of Mr. Goodchild (27).

2. *Inferiores.*

Metacarpo-digital Portion.—The feathers which constitute this series of minors are of such abortive growth that they are practically of no value for the covering of this part, and, as a consequence, no information is available with regard to the order of their renewal.

Cubital Portion.—The feathers of this row, not so much on account of their diminutive size (being scarcely $\frac{2}{3}$ the length of the medians), but because of the method of their renewal, are well worthy of a more special consideration.

It would seem that, with the suppression of the major coverts on the underside of the wing in the Passeres, the physiological functions of the latter had been transferred to the next row, viz. the medians, and in the same way that of the medians to the minors. Both these series have their moult more accentuated and more in keeping with that of the higher equivalents of the dorsal surface.

The first appearance of the members of this co-series is somewhat earlier than that of their dorsal congeners in the very young bird. In Nos. 7, 8, and 9, for instance, all very young individuals and of early dates, this row moults in advance of the dorsal one. Singularly enough, in the three specimens mentioned, the renewal begins at the carpal flexion, and proceeds inwards, which is in an opposite direction to the renewal of the dorsal series. This fact therefore foreshadows the ultimate method of moulting in groups, and is significant.

Specimens 5, 11, and 12 are examples of the earliest, or caducous, mode, in which the inferior row is developed strictly in synchrony with the members of the dorsal row. No. 12 makes an exception, perhaps, so far that the coverts of the inferior row are all in a nascent state only, and they are consequently in arrear of those of the dorsal row, whose components have developed $\frac{2}{3}$ of their ultimate length, and symmetrically from the two wings.

The transition from the premature to the fully mature condition of moult is a very erratic one for the whole series. In the few specimens, however, which show such evidence of transition, as, for instance, Nos. 13 (both sides), 15 (right side only), and 16 (left side), group-moulting sets in first, sometimes for the proximal, sometimes for the distal group, and in one case contemporaneously for both these groups; whilst the middle group, consisting of coverts 7, 6, and 5, does not appear to be affected until much later.

In any case, asymmetry seems to be a conspicuous feature in the replacement of this set for the individuals undergoing transition from the juvenile to the mature conditions of the moult. The coverts of this, as well as those of the dorsal series of minors which are allied to the remiges of group III., namely 7–5—*the last to change in every case*,—moult in advance of the latter. This is well seen in all the specimens

from Nos. 17–23, neither of these individuals having as yet acquired remiges IV., V., and VI.

Approximate Tabular Arrangement showing the Development for the Dorsal and the Ventral Series of "Median Coverts" during four consecutive Perennial Moults.

		Rows.	Groups.	Sets.	
Supply	Simultaneous	1st	2nd–4th	1st	Season.
	Gradual	2nd–4th	1st–2nd	2nd–4th	,,
Movement	Anachronous	1st–2nd	1st–3rd	1st–3rd	,,
	Synchronous	3rd–4th	3rd–4th	3rd–4th	,,
Development	Asymmetric	1st–2nd	2nd–3rd	1st–3rd	,,
	Symmetric	2nd–4th	4th	4th	,,

VII.—Summary of the Order in the Perennial Moult of the Wing-feathers.

The Remiges.

Two distinctly different principles in the order of the shedding and eventual replacement of these feathers are conspicuous. The first is that of the regular sequence of their renewal on the hand-portion from within outwards, though accelerated in certain places or retarded in others, in order to maintain the requisite balance for flight, by a system of approximate symmetry for the whole wing during this critical change. This is the principle which forms the rule for probably the entire Order of the Passeres.

But it is by no means the expression of the real morphological process of development which takes place, as we shall have an opportunity to prove further on when studying the behaviour of the covert-feathers during the moult. The true morphological principle is probably concealed beneath this purely secondary feature. In less highly organized birds, such as the Picariæ, an earlier and more primitive mode, namely, that of starting the moult on the manus from two separate points almost simultaneously, has been observed by Wittmer Stone (44), in the case of the Kingfisher, who (on p. 112, *l. c.*), after remarking on the principle of his "Order of Molt," writes thus:—

"Following these [the two innermost primaries] the primaries are shed at short intervals, one at a time, finishing with the outermost. *Exceptions I have noticed to this order in the Belted Kingfisher*[1], *Ceryle alcyon*, and the Snow-Bunting, *Plectrophenax nivalis*"[2]. And further on (p. 113, *l. c.*):—"The Kingfisher is strikingly

[1] These *italics* are mine.

[2] Wittmer Stone, on p. 113, also quotes the case of a male *Piranga*.

different from any other bird examined in that the *first wing-feather molted* is the *fourth primary*, followed successively by the *third*, *second*, and *first*[1] "*.

This same rule the author seems to have verified on the hand of three specimens in the same stage and coming from the same locality. But he continues :—"*How the molt proceeds*[1] after the first primary is shed, I am unable to say, *though the fifth*[1] [our VI.] is probably the next to be renewed, followed by the others in regular order inward."

It was my good fortune, when in Australia, to procure, as the first bird which I collected for this purpose, a fine specimen of a Brown Kingfisher or Laughing Jackass (*Dacelo gigas*) about the middle of the annual moult, so I am glad to be able to supplement the information desired on the point. According to my observations, the moult proceeds on the hand-portion—after having done so from the 7th outward—by immediately starting with the innermost or primary I. In the specimen observed by me this feather was nearly fully developed and further showed the *second* or next innermost in full process of moult, and the *third* cast off, preparatory for the renewal of this remex. Primary I., therefore, is the centre from which this section of the manus begins to moult next. This section comprises metacarpo-digitals I., II., III., IV., V., and VI. Although this section moults in arrear somewhat of the outer one, comprising VII., VIII., IX., X. (and XI.), yet, apart from its inner position, from a morphological point of view, it has to be considered as the first of the two.

I have elsewhere alluded to this arrangement as being overshadowed by a later principle in more specialized birds; similar signs as those referred to here for the remiges exist in some of the series of the coverts of the metacarpo-digital portion, and this is the same primitive principle as carried out more generally on the cubitus.

Gerbe (23), on p. 290, *l. c.* (see also *anteà*), was the first to point out a deviation for the forearm, from the linear progress of the moult of flight-feathers on the hand-portion; he, however, confined himself to this statement merely :—"Elle se manifest à la fois sur les deux points extrêmes du cubitus et prend deux directions qui tendent l'une vers l'autre." Beyond this he did not pursue their order of moult.

This I shall deal with in the course of my remarks on "Groups." As the initial diagrams A, B, and C show (Plate XXXVI.), the first one of these groups in which the moult sets in embraces cubital remiges VIII., IX., and X., which are renewed in the order of these numbers—that is, in a proximad direction.

Meanwhile the moult has set in also on the other extremity, beginning with cubital remex I., and by assuming the same inward direction as the group previously mentioned. This it does as far as the fourth quill, which forms the last one belonging to this group.

[1] These *italics* are mine.

* Wittmer Stone counts from the tip inwards, so that his *fourth* is probably the *seventh* (possibly the eighth in an eleven-primaried bird), after our reckoning; his *third* our *eighth*; his *second* our *ninth*; and his *first* is consequently identical with our *tenth*, at any rate last and outermost.

The latter, which I refer to throughout as Group II. (comprising remiges I., II., III., IV.), consequently forms the other "point extrême" of which Gerbe speaks. We have disposed, then, of two groups, whose remiges severally tend in the same inward direction for their moult.

This leaves us with a balance of three flight-feathers situated between the proximad limit of Group II., viz. remex IV., and the distad limit of Group I., viz. remex VIII. The moult, however, of the remiges of this centrally situated, or Group III., *proceeds in an opposite direction* (that is, in inverse order of their numbers), namely by beginning with remex VII., then VI., and by closing it with V. In the chart (Table II.) prepared for the chronological movement of the remiges (further see diagrs., Plate XXXVI. &c.), their alternate directions of moult are indicated by darts, pointing in the respective direction of their renewal.

In this way the order of the moult of each flight-feather itself becomes a definite unit of the group to which it belongs.

Similarly, as has been explained, each group itself becomes a definite unit in the cubitus as a whole.

Consequent upon the synchronous appearance of two or more group-integers, the numerical order in the replacement of the flight-feathers within the cubital portion as a whole breaks up.

The Tectrices.

The renewal of the wing-coverts presents some notable deviations from that of the flight-feathers.

Whereas the latter adopt the ultimate plan of renewal in sections immediately in their first perennial moult, the wing-coverts do not follow this same principle so soon, except by means of a series of transitory stages. These latter form a system of complexity in which two entirely different morphological features seem to mingle with each other: the one an early horizontal or diagonally longitudinal, and the other, later one, consisting of a transversely diagonal one for renewal.

As might have been noticed, a certain amount of difficulty occurred in tracing out the two systems of development. However, in following up step by step the order of renewal of the coverts—providing an extensive series of individuals be consulted on this point—all the conditions in the physiological process of their perennial moult may be found for discriminating between the various phases which produce this state of complexity.

But in order to better comprehend the degrees of complexity attending this interesting morphological question, it has become necessary to refer to some of the statements made on the subject of those writers particularly whose works have appeared in more recent years.

The observations made by Gerbe (23) on the simultaneous shedding of the principal coverts for the hand-portion of the wing have been described fairly correctly by

him on p. 290, *l. c.*, thus:—". . . leurs grandes couvertures qui sont pour le vol un élément important *les accompagnent toujours dans leur chute*" [1]. These researches led him also to the statement, recorded for the first time, of the two opposing directions which these coverts on the cubitus pursue for their renewal, as the flight-feathers; and further that here (on the cubital part) they are developed *in advance of their respective remiges* (see p. 290, *l. c.*).

To what extent this latter and more general statement is correct may be verified from the facts as they appeared in connection with the part dealing with these feathers. The degree of advance, as could be seen, depends upon the age of the individual. The moult of the coverts also follows the direction of the flight-feathers. This direction is not one of opposition from the extreme points of the forearm, but one which converges for the distad and the medial groups, and one which diverges for the latter and the innermost group. Gerbe did not investigate the appearance of the minor series of coverts.

Chalmers Mitchell's (12) interpretation of the longitudinal appearance of the flight-feathers and their principal coverts is that they are the co-serial members of a diagonally transverse arrangement with the other coverts, like that existing for the scaling in Reptiles, and as further diagrammatized by him in his text-figure on p. 232, *l. c.* This on p. 230 he explains thus:—

". . . . the quills and major coverts appear first as horizontal rows. It is only when these become obvious, and when one or two other longitudinal rows appear from before backwards, that the diagonal rows begin to be marked, &c."

And continuing further:—

". . . . I am not, however, prepared to attach great importance to this early ontogenetic appearance of the longitudinal rows as such."

As the result of this investigation also shows, there is in reality a marked transverse or vertical element entering into the composition. Though but faintly indicated in the chick's first perennial wing-feathering, it gradually increases with every subsequent moult by which the bird attains to perfect conditions of maturity and age. This transverse arrangement is a survival, therefore, of the phylogenetic affinities which link the present Class Aves to their Saurian ancestry.

The horizontal or longitudinal sequence of growth of the rows, applied to every series of the coverts (as well as the main quills) in their entirety, is the result of a secondary provision, and of a purely ontogenetic origin, which is assumed by the embryo and the young bird for its first set of wing-feathers.

Afterwards this same sequence of renewal becomes restricted to those sections of the rows which form part of the several groups on the forearm. Within these groups the horizontal renewal is retained throughout every moult. Each of these three sections performs this longitudinal process independently of the other two.

[1] The *italics* are mine.

The great importance which attaches to the covert-feathers in helping to clear up outstanding questions connected with the evolution of the organ of flight was fully recognized by Mr. Pycraft (39), who has approached the subject of the origin of *Diastataxy* from the point of view of Embryology. In the course of his description of the "Embryo Wing" (see p. 239, *l. c.*) he says, for instance:—"The movement of the remiges is in all cases accompanied by a corresponding movement on the part of the coverts associated therewith, from the post- to the pre-axial border."

And continuing, he says:—"The result, when the wing is viewed as a whole, seems to show that a process of 'faulting' has taken place, &c., &c." This process of *faulting* or *shifting* he, moreover, supports by an ably devised diagram (see p. 239, *l. c.*).

It is really the first indication of a transverse rearrangement of the rows at this early stage of development. That it is a totally distinct feature from the longitudinal principle of feather-supply is equally endorsed by this author, who initiates, on p. 238, the paragraph treating of the subject by the following words:—"In all wings the feather rudiments appear first along the post-axial border of the wing; those representing the remiges and their major coverts appear simultaneously, and sometimes together with very faint traces of one or more of the pre-axial rows representing the median and minor coverts." And further:—"The change takes place, however, generally at the close of this phase of development."

Now it is this "faulting" precisely on which Goodchild in his researches has laid so much stress, and which has supplied this author with such a solid basis for his observations on the coverts of the cubitus. Further evidence of a transverse character he has clearly also shown to exist in the alternate imbrication of the members of certain series of coverts, which is so conspicuous a feature in a great number of families of birds. Similar indications of this principle may be found to exist also in the shape of the permanently shortened coverts which mark the various sections of this portion of the wing for some families of birds (Degen (16), p. xxiii). Their places almost exactly correspond with what we have learnt through the conditions under which they moult.

The appearance of a first set of wing-feather-plumage is an endowment of secondary origin. It is the common bondage for all Carinate birds. In the *Chenomorphæ*, for example, this early ontogenetic mode of feathering is repeated more or less in every moult (*anteà*, p. 366) for both portions of the wing.

In more highly organized forms, however, this latter mode is confined merely to the very young individual on the cubitus, in which, with every succeeding annual moult, the transverse character of primitive origin comes into prominence.

The latter reveals itself also by the moult of both the flight-feathers and the coverts on the metacarpo-digital portion in some families of the *Picariæ* (Kingfishers); whereas in the *Passeres*, whilst being merely concealed by a chronological difference

for the remiges and the major coverts of this portion, it is wholly retained by the median, and in part by the minor series of coverts still, as evidenced through their moult.

VIII.—The Contour Feather-Tracts, or Pterylæ.

Preliminary Remarks.

No really so precise a description of the order which the moult pursues in these tracts is possible as that which enabled us to follow it for the "alar tracts."

One reason for this is that synchronous renewal is not circumscribed so definitely on the body as it is on the wing. But on this head I cannot do better than quote Dwight (17), whose statement, p. 84, *l. c.*, under the heading of "Advance of Moult in the Feather-Tracts," is as follows:—

"The only way to get any idea of how a moult proceeds is to appreciate the fact that it begins almost simultaneously at a number of points in the different tracts, and advances independently from each of them. This is why a bird seems to be moulting at irregular spots all over. There is, as might be expected, a good deal of individual irregularity in the growth of new feathers, *but when each tract is studied separately, each will be found to have a definite plan of development* [1], which in its turn fits into the general scheme of the process we call the moult." And, again, in connection with this subject on Gulls and Terns (18), as regards "Sequence of Moults and Plumage of the Laridæ," he says (p. 50):—

"The moults occur at definite periods, and the feather-growth spreads from definite points in the feather-tracts, so that nothing is a matter of chance unless it be the arrested development that befalls all organisms, and occasions in birds the retention of old feathers among those that are replaced by new ones at time of partial moult."

The above statements so exactly describe the conditions that exist in the species under consideration that I can add very little else to them as the result of my own investigation. In consequence, this account can be restricted to the narrowest limits by merely pointing out a few specific deviations from the broad principle.

A second reason for not being able to make a comparative survey of the moult in the various body-tracts consists in the technical difficulty presenting itself of dealing with them simultaneously, the same as they are in moult. This difficulty is further enhanced by the fact that this not only applies to the tracts themselves, but, as pointed out by Dwight (see *anteà*), to the different parts of a tract by the new growth which spreads in both a diagonal, transverse, and longitudinal mannner.

Having, moreover, early recognized the desirability to adequately express in some manner of form the complex order of moult, besides the systematic description of the different tracts, I have prepared a chart (Table VI., p. 398) as the only alternative for intelligibly conveying the relative order of their moult.

[1] The *italics* are mine.

In this chart are entered all the tracts and the various longitudinal rows of feathers of which they consist. The rows against which an asterisk has been placed are those which form centres from which the moult proceeds. The pointed ends of the blackened bars denote approximately the beginning of moult of that particular row of feathers. The time of the completion of the moult for the same is indicated at the point where the shading reaches its maximum by filling up the space between the parallel lines which divide it from the neighbouring bar.

Beginning and completion of the moult of each row is measured by the common standard, namely, that of the development of the *Metacarpo-digital Remiges*, whose numbers in this order from right to left are placed at the head of the Table, as are also those of the *Cubitals* and the *Pennæ pollicis* for chronological comparison. A similar arrangement has been provided in this table for the rectrices and their coverts at the bottom.

The Spinal or Dorsal Tract (Pteryla spinalis).

This is of a well-defined Passerine form, and partakes of the type under which "Nitzsch" (37, pp. 79 & 80) subordinates Cuvier's Group of the Dentirostres as follows:—

"A. With 12 rectrices.

"*a.* Saddle without a space.

"1. *Barita.*—. . . . saddle short, broadly rhombic, acute angled. *B. strepera*, *B. destructor*, *B. varia.*"

But it also partakes in part of the description which follows for the characters applying to his second division of this group, between which it seems to fit in, namely: "2. *Thamnophilus*, seu *Vanga*, and *Lanius*, species *undulatus* and *procerus*," in which he refers to "twenty remiges which are all very broad and obtuse, graduated as far as the fifth [our VI.], which is of the same length as the sixth [V.] and seventh [IV.]." . . . . And further: ". . . . the saddle is heart-shaped reversed, emitting a single row of feathers from its middle as the commencement of the rump-band."

From this definition of the rump-band *Gymnorhina tibicen* deviates by emitting not only this single row, but two additional ones as well, whose feathers alternate by means of quinqunx from 3 to 2 for about 7 or 8 of these sets, from whence a short distance backward to the oil-gland the tract broadens further out into two more additional rows, making 5 in all.

The saddle portion itself in its widest diameter, which is placed two-thirds backward, consists of 12 rows, tapering out to 6 rows on its anterior or interscapulary portion, which further in front widens out into from 2 to 3 additional lateral rows, from which latter region it broadens out into the head tract.

I have found the moult to proceed from three distinct main centres on the principal

part of the spinal tract, and it affords me great satisfaction to have independently arrived at the same result as that of Mr. Dwight, whose paper I did not see until towards the close of my work.

Of these, one proceeds from the lumbar, one from the thoracic, and one from the interscapulary region (this latter beginning to moult later: see Chart, Table VI.). In addition to these main centres, there is to be noted another for the portion to which I refer as "the Lower Neck Region" in the Chart. I have also pointed out the lateral rows as such, from which moult proceeds later, as a secondary feature.

I am also able to state that I had a similar notion about the agency of the blood-supply possibly influencing the early moulting conditions of these centres, as referred to by Dwight (*l. c.* p. 84), to which the specimen No. 12 testifies, and from which the present description of this tract is made, by having used a carmine injection for the purpose. In this I failed to procure the desired evidence, on account of some unsuspected internal injuries by shot.

From these main centres the moult spreads both forward and backward simultaneously, but slightly more in proportion in the latter direction. It shows signs of energetic progress nearly always in advance of any remiges, as shown in my earliest acquired specimens. It is also protracted during and often beyond the latest phases of development of flight-feathers, as specimens in which the moult of the latter is completed show. The middle row is in full vigour of new growth, and approaches completion much sooner than the time of appearance of primaries III.–IV., as shown on the Chart; the crown of the head, and notably the auricular regions (lores, &c.), being the latest of the lateral rows to change, except the sides of the nape.

The Humeral or Scapulary Tracts (Pterylæ humerales).

Pterylographically, this tract, which is a double one, has been defined by Nitzsch (37, p. 25) as being entirely divided by space (the lateral *Apteria spinale*) from the spinal tract previously considered. Although being more directly connected with the "inferior tract" by means of a band of closely-set rows of feathers, it is linked, nevertheless, in this particular species to the "spinal tract" by a contiguous set of softly-textured feathers consisting of about three rows. These are placed across the clavicular region in front of the head of the humerus, thus bisecting the long spinal apteria, a similar arrangement as that ascribed to some birds by Nitzsch (p. 25, *l. c.*), e. g. *Steganopodes*, *Buceros*, and *Colius*, which, as he remarks, "may nevertheless be recognized as distinct tracts by the stronger formation of their feathers."

The humeral tract may be subdivided into two distinct portions, each with a well-marked centre from which the moult spreads independently, a humeral and a clavicular, or more marginal portion, the latter merging into the alar marginal tract. Both these consist of several rows after their bifurcation. Of these, those medially situated are

affected earliest, and simultaneously with the corresponding rows of the spinal tract; the internally and externally situated ones which compose these branches begin to moult somewhat later, about the same time as the renewal of primary remex III.; this is also the case with the lateral rows of the thoracic portion of the spinal tract. The moult for the feathers of this tract on this part of the body sets in most vigorously, and is achieved at a comparatively earlier period than that of the dorsal main stem.

Closely allied to the distal rows of its humeral branch are the feathers which compose the "Parapterum." Only a narrow space separates the two. The feathers of the latter take up the moult from the humeral branch, and in younger birds are replaced by synchronous appearance, whereas in older individuals they are renewed in more regular sequence from within outwards.

The more marginal branch spoken of, and entered also in Chart (Table VI.) as "clavicular," follows the same principle for the moult of its feathers as that which applied to the former branch. Its distally situated rows on the underside of the wing establish a connection with the "Hypopteron," from which it is but slightly separated also. The feathers of the Hypopteron, which are a somewhat rudimentary set (being of a filo-plumaceous structure), begin moult—which is always a simultaneous one for them—later than those of the Parapterum, their appearance corresponding with the renewal of primary V.

The Inferior or Ventral Tracts (Pterylæ gastræi).

Commencing with the chin, and covering the throat in one homogeneous mass, together with the head and sides of the neck, with which portions it coalesces, this tract divides itself into two stems in the gular region, which descend in a laterally-curved line towards the anal region, without, however, reaching the orifice. These two stems enclose the *apterium mesogastræum* of Nitzsch (p. 34, *l. c.*). Excepting the portion of the throat mentioned above, its rami may be further subdivided into "pectoral" and "inguinal" portions respectively. The former are of considerable width, and consist of about from eight to ten longitudinal rows of feathers in their broadest parts. These send off the lateral extensions, backward and outward, referred to by Nitzsch (*cf.* p. 27, *l. c.*) as *pterylæ laterales*, more prominently perhaps in the species under examination than in those Passerine forms referred to by the latter author (*cf.* pp. 28 & 80, *l. c.*). These small ramifications set off distinctly enough immediately in front of the portion which forms the greatest expanse in the double tract just below and posteriorly to the arm-pit.

At a place slightly in advance of the junction of the latter with the main pectoral portion is the principal centre from which the moult proceeds longitudinally backwards, and to both sides of the tract, by renewing every alternate feather, sometimes overlapping two feathers in either direction. The inner rows of this portion moult with great rapidity during the earliest stages of the complete feather-change; whilst

EXPLANATION OF TABLE VI.

In the 3 divisions above the *horizontal line*, which is extended to the left, are entered the flight-feathers of the *Alar tract* in the order of their moult from left to right.

The metacarpo-digital remiges or primaries for which the Roman figures I.–X. (XI.) have been substituted are placed in the *top portion* of the lower division and serve as the chronological scale by means of which the moult of all the other tracts with their component rows may be compared.

The *lettering* in the portion below this and immediately over the line corresponds with the lettering for the metacarpo-digitals in Tables I. & II. and Plates XXXVI.–XXXVIII.

The Roman figures in the *lower portion* of the *middle division* show the synchronous replacement of the cubital remiges or secondaries with any of the primaries in moult. They are lettered with dashes thus: ', '', ''', in conformity with that of Tables I. & II. and in Plates XXXVI.–XXXVIII.

Above these and in the *uppermost division* in ordinary cyphers are placed, according to their order of replacement, the *Pennæ pollices*, synchronous in position of their moult with those of the respective remiges.

Each *shaded bar* represents the moult of the respective row or rows of feathers, denominated as such to the left of it.

Its *pointed end* indicates the commencement of the moult of the row of feathers which it represents.

The *tapered portion* of the *bars* from the tip to the angles which its sides form with the parallel divisions of horizontal lines, shows the comparative amount of moult for that row.

At the *place* where the *shading* fills up the parallel divisions, the moult of this row of feathers is completed.

By means of the *vertical division lines* their respective stages of moult may be read off on the scale provided for the moult of those remiges with which these stages coincide.

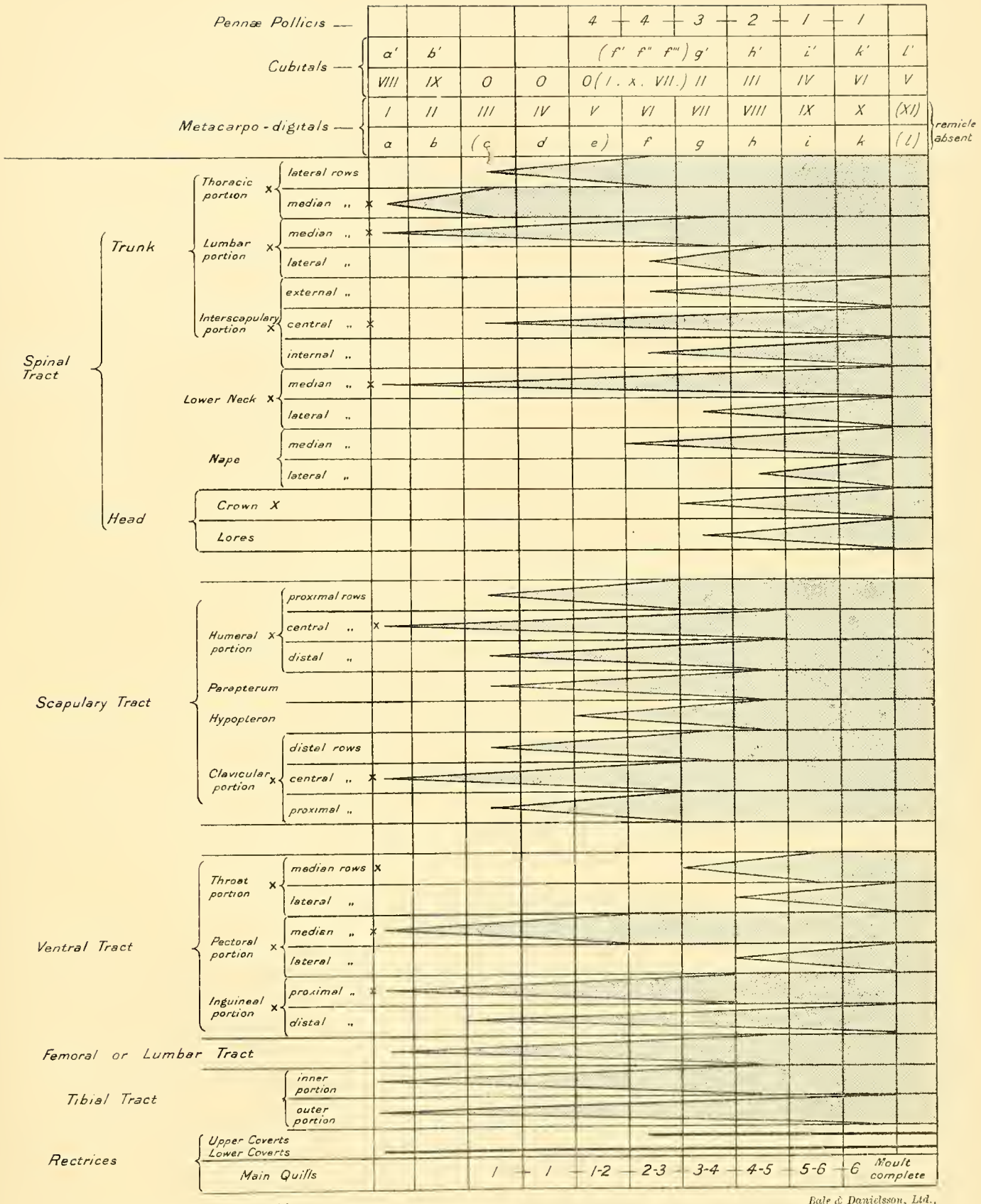
A × against a unit of rows or a particular row signifies that this is a particular centre from which moult proceeds.

The rows which constitute a tract are bracketed together and are headed by the pterylographic name of their respective position.

The latter are bracketed together again according to their anatomical position on the bird, and denominated as such at their head.

The *division* at the *foot* of the Table is devoted to the synchronism in moult for the *tail-feathers* by means of *bars* for the *coverts*, both dorsal and ventral, and by their respective numerals for *main quills* or rectrices.

TABLE VI.



E. Degen, del. Hale & Danielsson, Ltd.,

Chart showing the correlation of growth amongst the feather tracts during the period of the moult.

the lateral rows, both internal and external ones—to which latter the pterylæ laterales belong,—do not take up the change until considerably later, viz. the stage of renewal of primary remex VIII.

The centre of moult from the other, namely, that of the "inguinal" or gastric portion—which is a continuation of the pectoral one, consisting of three or four rows of feathers only,—begins also synchronously with that of remex I., or directly after. The progress of renewal of the feathers of this portion is much slower, though slightly faster in the case of the innermost rows than the lateral ones. This condition points to the fact that the inner rows are really equivalent to the median ones of an undivided tract.

The third centre of feather-renewal for this tract is at the point of bifurcation for the two pectoral *rami* on the lower throat. Contrary to the mode of moulting, in an antero-posterior direction, of these latter, the moult of this portion proceeds in a forward direction only, until it finally reaches the *mentum*. It is not till much later on in the season of general moult that it sets in here; but when it does, it happens in a vigorous manner, which is about the time of remiges VI. and VII. for the central rows. These are followed immediately by the outer rows, which complete their moult at the time of renewal of cubital remex V., the last of the flight-feathers to moult.

The renewal of the feathers of this tract in the order in which it has been described here is that of the older individuals. In younger birds this order is not so clearly defined.

The Femoral or Lumbar Tracts (Pterylæ femorales *seu* lumbales).

These are composed of two rows, consisting of nine or ten soft and elongated contour-feathers each. They are renewed in alternate rotation—that is, by beginning in the superior row with the feather which is situated nearest the *apterium spinale*, to be followed by that of the inferior row next to it, and from whence the feathers are renewed in tolerably regular sequence in backward direction. Though the feathers of this double tract are only few, their renewal, which begins with the earliest phases of the flight-feathers, is not completed till about that of remex VIII.

The Crural or Tibial Tracts (Pterylæ crurales).

Both portions of these tracts, which clothe the tibia—an inner and an outer one—and which are separated in their upper or femoral portion by an apterium, merging with each other below the knee, moult simultaneously. The moult begins early and synchronously with the centre of moult of the other tracts, from above below, and finishes on the tarsal joints. The time of completion corresponds with the last stages of flight-feather renewal. This is somewhat remarkable for a tract which consists of so few feathers, seeing that their renewal begins at a comparatively early period of the perennial moult and finishes so very late.

The Rectrices and their Coverts.

The tail-feathers are replaced in a perfectly regular order from within outwards, as are also their coverts, both dorsal and ventral. These coverts consist of two rows each, equivalent to the major and the median coverts of the remiges.

The first or innermost pair of rectrices—of which it is sometimes the left, or as in some individuals the right side, which moults first—is renewed at the time of renewal of primary remiges III., IV., and V., or the triplet marked *c*, *d*, *e* (see also diagram, Plate XXXVI., and Tables I. & VI.), as has been pointed out.

About the time of renewal of the 5th primary, the second innermost pair of rectrices takes up the moult, generally before the first is completed, and, with the next remex in moult (viz. primary VI.), the third pair follows suit, and so on; the last and outermost sixth pair coincides generally with the two outermost metacarpo-digital remiges IX. and X.

Frequently there are as many as three pairs of tail-feathers to be seen in various stages of graduated length of renewal, but, as a rule, there are not more than two. The former condition occurs in younger, whilst the latter is the case for older individuals. Their dorsal coverts take up the moult somewhat later than their ventral ones, which latter are amongst the first feathers to renew of the whole plumage, as may be seen, by their relative order to the rectrices, at the bottom of the Chart (Table VI.).

IX.—Conclusions.

Having, in the preceding pages, described the chronological behaviour of the feathers during the moult of the individual, and further shown, with the help of diagrams and tables, the relationship of their development to one another, by paying special attention to the principal feathers, I can now proceed with the explanation of my views with regard to the manner in which they reflect the phylogenetic conditions of the archæornithic type from which the wing of the modern bird has been evolved. For this purpose it becomes inevitable to refer again to the details of the theory propounded in the pages of my former work (16) and notably so to plate i. fig. 3, *l. c.*, for the views there brought forward.

The present investigation gives me no cause for materially altering the fundamental plan laid down in the former paper, other than two slight modifications. The first and principal one, referred to already under the part headed "Ala spuria," is the result of the additional discovery of the inverse order in the shedding and eventual replacement of the *pennæ alares* of this portion, as affording us a *likely key* to its further solution. The other point is one of a merely subordinate character, and I propose to allude to it later on.

Immediately on entering upon the question, our attention once more gets directed

towards that point which forms the focus in the whole problem, viz. the *diastema*, for the position of the 5th cubital remex. The space between the first primary remex on the metacarpus and the sixth secondary one is occupied by cubital remiges I.–V. (exclusive of a carpal vestigial one), with their respective main coverts, which form the most distal group on the forearm, and here spoken of as Group II., on account of the moulting of these feathers second in order, and therefore in keeping with this particular feature.

All the members of this group moult in inverse order, viz. from the wrist-joint inwards. To these, in my former diagram (pl. i. fig. 3, *l. c.*) of the reconstructed wing, was allotted a metacarpal position; and, in allusion to their possibly former digital derivation, they were referred to as "proto-metacarpo-digitals."

The significance of a similar fact of the "*pennæ pollicis*" moulting in an inverse direction, too, assumes now additional importance through this peculiarity. As mentioned before (p. 371; see "Ala spuria"), that it probably would matter little whether these feathers were regarded from a purely remigial or a tectricial point of view; this again finds corroboration in this place, since main coverts follow the same routine order of moult as do remiges. But what really transpires is (especially when taken in conjunction with the sectional moulting of the flight-feathers on the manus, as in the Kingfishers and others, and further shown for the dorsal median coverts in this species) that we have clear testimony in this of the presence of a distinct *digital*, and an equally distinct *metacarpal*, element. To the remiges of the former derivation therefore alone belongs the term *proto-*, whilst to the latter belongs that of *hypo-metacarpo-digitals.*

If then, as the principle of analogy would justify us in adopting, the same rule by which the remiges of the former Group II. (and now become our *Hypo-metacarpo-digitals*, or further abbreviated "*Metacarpals*") were applied to our permanent meta-carpo-digitals I.–X. (XI.) (or frequently more as in the Ostrich and probably in the archæornithic wing), the only possible inference would be that these latter are those of purely *digital* origin.

As such then, and the fact that both sections of which the series is made up, viz. from I.–VI., and the other from VII.–X. (XI.) and moulting both in an outward direction, it is these which now become our true "Proto-metacarpo-digitals" of the hypothetical wing.

In the "modern wing" those of the outer section alone, namely, primary remiges (VII.?) VI.–X. (or XI.), deserve henceforth the appellation of "Permanent Digitals" (see former diagram). On the other hand, the primaries of the inner section, viz. I.–VI. (having, in association with synostosis of the metacarpal bones belonging to digits II. and III., been borrowed from their previous phalangeal position on digit III. by the now combined metacarpal bones with which they have become

permanently associated) deserve to be called "permanent" only in so far as they are derived from the same source as the former.

All that remains to be further explained now, after having shown their purely digital value, are those *digital phalanges* on which they were originally situated. These could have been none other than those belonging to digit III., as we shall see.

The crowding together on the wrist of the flight-feathers in their backward-shifting process towards the elbow caused the forearm to receive first the quills originally belonging to digit IV. Next to these followed the "metacarpals" belonging to digit III. This must have occurred contemporaneously with the process of ankylosis of the two metacarpal bones, so that these "digital" remiges in question and belonging to digit III. found the channel obstructed by their former neighbours, the "metacarpals" mentioned above, which had preceded them in this course of shifting into their new position on the forearm and in the latter of which they became fixed. Hence, in the same manner, they became fixed themselves, in turn, on the combined metacarpal bones.

Another peculiarity which has often arrested my attention also seems to point strongly to such a rearrangement. It is that of primary digital remex VII., or, anatomically speaking, the "addigital," which, instead of having its base inserted, like those of VIII., IX., X., or XI., on the phalanges which bear them, crosses the retained terminal phalanx of digit III. entirely, to insert itself above it, together with the shafts of all those from this one inwards, on the metacarpal bone of digit II. This arrangement is also distinctly shown in Wray's (46) text-figure on p. 351 (fig. 2 *a*, *l. c.*) for the faithful drawing of the wing of an adult Ostrich, in which bird, owing to the greater relative length of this complex terminal phalanx, the shafts of no fewer than three primaries likewise cross it.

A reference also to my former diagram (table i. fig. 3, *l. c.*) shows that in this I suggested, by means of dotted outlines, a suppositional remex to have been present, as well as that of the "carpal remex and its covert"; it is marked there I′, and × on phalanx I. of digit III. When this digit was probably slightly inferior in length to digit II., but otherwise composed of the same number of phalanges (see also Wray, (45), p. 284, "Note on the Vestigial Structure in an Adult Ostrich," figs. 1–4 representing the digital phalanges of digit III.), it was doubtlessly capable of giving accommodation to a similar number of remiges like that composing the inner section of the primaries, as in the present forms of birds. In fact, Wray shows this number to be equal for the Ostrich, namely 8 "metacarpals" and 8 "digitals."

The next point of difference to account for concerns those flight-feathers on the cubitus which compose Group III., the last to moult, and comprising secondaries VII., VI., and V. In my former drawing the metacarpal bone of digit IV. is represented as carrying one remex only, namely cubital VIII.

Having seen that IX. and X. also moult in an inward direction, the inference from

this would be that this bone was probably the carrier of more than that remex VIII. by further including IX. and X. also.

Inferentially, from their outward order of moult, both VII. and VI. being of digital origin, their position on the first phalanx of digit IV. would require no other alteration to my former diagram, except perhaps the cubital remex V.—which, according to its moult, seems to belong to the set of flight-feathers composing Group III. (further shown in the scheme on p. 404)—takes up the outermost digital position of digit IV. instead of the most inward metacarpal one to which I then assigned it.

For exactly the same reasons "carpal remex and covert" become "last metacarpals" of digit III., instead of being, as interpreted previously, "first digitals" of the same finger. It is merely a shifting backward by one place *in toto*, with the further consequence that "cubital remex V." of the specialized Passerine forms requires to be also theoretically included with the remiges (0 carpal remex) I.–IV., our present Group II. and the most distal on the forearm, by means of this disposition.

Indeed, the greatly vacillating position in the order of its renewal which this flight-feather takes up makes it difficult to determine whether it moults last of Group II. or first of Group III. It seems from four specimens (Nos. 24–27 of diagrams, Plate XXXVIII., left and right wings) that it is connected directly by moult with the remiges of the distal group in Nos. 25 and 26; whilst in No. 24 it holds a position strictly intermediate, the new-growth remiges IV. and VI. in the two wings of this specimen having been fully accomplished. Its determination as to new or old growth in specimen 27 being somewhat doubtful (see Table I. parts *a* & *b*, and also diagrams K, L, M of Plate XXXVIII.), the latter gives no positive information on this point.

This slight preponderance in favour of its closer association with the distal group is fully counterbalanced by the opposite condition of moult of this remex in specimens 28 and 29, which were both received on a later date, namely March 20, and preserved in a dried condition on account of their almost completely finished moult. But the following notes on these, taken down when fresh, will confirm the above:—

"No. 28, ad. ♀, March 20.

"Remarkable specimen on account of its white back (albinism or hybrid between *G. tibicen* and *G. leuconota*?).

"Moult complete *with traces of same on wings* (both sides) *for cubitals* V. *and* VI. Incomplete on dorsal tract."

And for:—

"No. 29, juv. ♀, March 20.

"The *6th cubital* of the *right-side wing a little shorter* than *corresponding feather of left*. The *5th* cubital apparently the old remex not yet shed."

By preferring the incorporation of cubital remex V. of the Passerine type of bird with the distad group, we necessarily encroach upon the number of remiges of the middle group, viz. V., VI., & VII., which in this case would reduce this group to only

two quills, namely VI. & VII. Naturally, then, this would restore to the distal group the number of remiges allotted to them in my former diagram. And, in continuing this process of borrowing one remex from group to group backwards consistently, it certainly would have the advantage of bringing us in positive accord with the results arrived at in the compilation of my former diagram, namely by ending with secondary remex VIII.; thus leaving us with remiges IX.–X. to be disposed of as "remiges cubitalis veri."

But against the inclusion of cubital VIII. in the middle group is seen *the perfect constancy with which the latter remex begins the moult first in all the specimens*, to be followed in turn and with equal constancy by secondary remex IX. It is not till much later in the moulting-season that in Passerine species remex VII. begins its renewal, in fact not before VIII., IX., & X. are all nearly completely renewed.

The fortunate acquisition of the two wings of a Moor-hen (*Gallinula chloropus*) in just such a stage of moult, as well as numerous material of Parrots in the same condition (notwithstanding the fact that the former belongs to a eutaxic family of birds), shows that in these birds (a fact in which they all agree) *it invariably is the cubital remex* IX. with which their moult begins first on this portion of the wing.

Moreover, an examination by Pycraft (39) fig. 4, pl. 14, of the wing of a young fowl, convinces me that the "eutaxy" of the Gallinæ—and probably all those more primitive groups of birds which compose Mr. Pycraft's list of eutaxic forms (see p. 248, *l. c.*)—is morphologically not the same "eutaxy" as that of the Passeres.

The constancy with which in diastataxic wings moult sets in first with cubital remex IX., by commencing the renewal in an inward direction of the proximal Group I., against the commencement in the latter with remex VIII. of the Passerine mode, legitimately points to the assumption that these two quills are morphologically identical with one another, and that the cubital remex V., where it is present in such eutaxic forms as the Gallinæ and similar birds other than Passerinæ, is the original remex V. still retained by them.

The following scheme will further express my meaning:—

Scheme for right side of Wings.

	Group II.						Group III.			Group I.	
Galline eutaxy	(0)	1	2	3	4	5	6	7	8	9	*x.*
Numerical figures of cubital remiges	(Carp. R.)	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	*x.*
Passerine eutaxy	(0)	1	2	3	4	0	5	6	7	8 9 10	(11)
	Group II.						Group III.			Group I.	

Whether cubital remex V. in the Passerine type of eutaxy is really a member of the distal or of the middle group cannot be determined positively by means of the present material; but it will in all probability be found to belong to the latter, seeing that it takes up the moult more frequently from the 6th and not from the 4th. This is only what may be reasonably expected from a flight-feather which is actually remex VI., and numerically only remex V., as in the present species. Of the original remex V. in the Galline type of eutaxy, there is not much doubt as to its belonging to the distal group.

It has been suggested (see *anteà*, p. 401) that the inner section of metacarpo-digitals, at present situated on the combined metacarpal bones—on account of their eminently "digital" character,—were elements originally belonging to the digital phalanges of digit III. Since we have found in our former "*proto-metacarpal digitals*" (cubital group II.) *the true original metacarpal elements* belonging to the metacarpal bone of the latter digit, we see that this distribution leaves us minus a similar equivalent for the metacarpal bone of digit II.

From this the question arises as to what has become of this series, or are they really anywhere at all?

The answer to it is not so obscure, and is one to which Goodchild, Wray, and Pycraft have contributed.

The survivors of this set of feathers are present still in the diastataxic wing, and the older forms of the eutaxic birds, in the shape of that enigma of a part-series, which is situated on the distal portion of the forearm known as the "intercalary row." In the majority of those birds this row consists of from 5–6 feathers, but their number is reduced to 4 in some. If they are not actually the aborted flight-feathers themselves (as I suspect them to be, from the fact that in the specimen of a young Parrot—*vide* text-figure 2, p. 364,—contrary to the presence of sessile neossoptiles for all the other covert-feathers, the latter are, curiously enough, absent on both sides) they are at least the major coverts of the entirely suppressed remiges to which they belonged, and which are the set of feathers to be yet accounted for.

This latter supposition would constitute a case of "apoptilism" for the whole series, the same as applies to that of the *Parapterum* (Degen, 16). Of their pterylo-genetic relationship to the other covert-series on the dorsum, I would refer to Goodchild (27), in whose drawings they are marked by the letter C. Goodchild has found them to be such excellent landmarks for the determination of the rows that the following quotation from his paper gives a sufficient idea as to their value for further collateral evidence. This is what he says on p. 189, *l. c.*:—

"In the type of wing-feathers prevailing throughout all, or nearly all, the rest of the Psittacidæ (in speaking of an additional row of backward-lapping wing-feathers in *Melopsittacus*) an additional modification may be observed. The row of feathers

coming on next above the greater coverts, indicated by the letter C (*intercalary row*) in the following diagram, is seen to consist of a series numbering generally five or six, which are confined to the distal areas of the cubital region, and form a distinct and separate series from the feathers that extend across the median area. *They correspond in relative position to the upper wing-coverts* (t.m.) *in the manual region of the wing*" [1], &c. And further on :—"The feathers referred to often form a conspicuous feature on the wing of the living bird, as they are frequently arranged in such a manner that the shafts of three or more of the feathers are in a line. *The proximal edges of the feathers are generally as firm as those on the opposite side* [1], and, as a consequence, the whole series slides between the feathers next them on the proximal side in much the same way as the blade of a lancet closes in its sheath," &c.

Wray (46) also drew attention to this set of feathers, and after rectifying in his paper a few incongruities which arose out of Goodchild's nomenclature for the grouping of portions of the series on the wrist, dismisses the subject (p. 350, *l. c.*) with the following remark :—

" Grouping the feathers according to their insertion, and remembering the conditions of folding which must occur on the wrist, the observations of Goodchild give the most complete view of this subject we have."

It is in Pycraft's excellent thesis (39) that the greatest amount of significance as yet attached to the presence—better expressed *appearance*—of this set of flight-feathers called the " intercalary row " has been most signally pointed out. But how much the introduction of this element became responsible in the " shifting process " (chiefly transverse) of all the rows of the distal portion on the forearm, with its consequent " faulting," a glance at the drawing of his own preparation, of the nestling *Lomvia troile* (*cf.* fig. 2, p. 243, *l. c.*), suffices to show. He thus lucidly describes it :—

" The disturbance is much more obvious in the row of papillæ immediately above the remiges—the rudimentary major coverts 1–5. These have become distinctly separated from the rest of the row proximad of this point. The disturbance of the rows preaxial to this of the major coverts is barely perceptible. *There is yet no intercalary row* " [1].

Why, in spite of the impendingly disturbing influence they exert at this critical stage, he never so much as attributed to them *the real cause* of the general disturbance which his later stage (of the above figure mentioned) so clearly demonstrates, seems incomprehensible now, although clearly capable of explanation. The reason is that he connected them—upon their sudden appearance—embryo-genetically with the members of the rows of either the Medians, or those above the latter, *e. g.* the Minors, entertaining even some slight doubts about their serial value as regards the latter's first or second row; instead of treating them as the real cause which separates the

[1] These *italics* are mine.

Medians from the Minors between which they wedge themselves in. With regard to the unsteady location of this intercalary row, in describing on p. 242 (*l. c.*) the two different stages of the wing of a Lapwing (*Vanellus cristatus*, pl. 14. figs. 1 & 2) he says:—"It is of interest to note that the downward shifting in this case must have been but slight, *as the intercalary is the 2nd and not the 3rd row of coverts* [1], as was the case in the typical wing described on p. 239."

That there is still another peculiarity which attaches to this row seems almost a possibility, though not sufficiently clear as yet. It is that their position as regards the Parrots is undoubtedly immediately above the major coverts; this is confirmed by Goodchild; whereas, to judge from Pycraft's well-executed drawing of the wing of the young fowl and that of the *Lomvia troile*, they are unmistakably placed above the medians. I have no doubt about this interpretation as being correct also. But it seems to suggest one thing, and that is, that they originally wedged themselves in between different rows in different groups of birds, sometimes above, sometimes below the medians.

Their appearance takes place at a time when both the wing-membrane and the bones are still very plastic. While in this condition, the contact of the flight-feathers with the latter is much less intimate as far back as the region of cubital V., to which point hardly any impressions of the contact of the remiges with the ulna can be found. It is only proximally from this point that the bone shows traces of their contact in the shape of sockets consisting of pits and tubercles, which are retained throughout all the moults, and which are the outcome of the early fixtures of the remiges on the posterior portion of the ulna.

If the feathers composing the group of intercalaries were derived from the minor series, the order of their renewal should correspond with these latter, which is an outward one. Such, however, is not the case, as seen in a specimen of a Parrakeet (*Platycercus eximius*) in my collection, and dated from March 4, which shows this particular stage of moult. In this the renewal proceeds in the same inward direction as do the flight-feathers, their major and median coverts,—all belonging to the distal group. On its right-side wing the 3rd, 4th, and 5th, or most proximally situated feathers of this intercalary row, are to be seen in successive stages of growth in the numerical order quoted; whilst the 2nd and 1st respectively, or more distal ones, show unmistakable signs of their having quite recently attained full development. On the wing of the other side, this stage of moult is slightly more in advance, the 6th or last feather being in process of renewal only.

A specimen of a Musk Lorrikeet (*Glossopsittacus concinnus*) also shows the same arrangement. In consequence of this fact, the significance of flight-feathers as an additional integer requires to be placed upon this set of feathers, similar to the

[1] These *italics* are mine.

remiges I.–IV., with the further definition, however, of a former "metacarpal" derivation.

The following scheme will be found to supplement the original distribution of the flight-feather elements on the fore limb of the ancestral bird, according to the evidence adduced in its favour through this work. It represents the left-side wing.

Revised Scheme for the Derivation of the Flight-feathers from the Tetradactyle Ancestral Form of Birds.

Proto-metacarpo-digitals = Flight-feathers of Phalangeal Origin.	*Hypo-metacarpo-digitals* = Flight-feathers of Metacarpal Origin.
Digit I.	
Suppressed (lost).	Present Pennæ pollicis IV.–I.
Digit II.	
Present Metacarpo-digitals XI.–VI.	Present Intercalary row I.–VI.
Digit III.	
Present Metacarpo-digitals V.–I.	Present Cubital Group II., Secondary Remiges (0) I–IV.
Digit IV.	
Present Cubital Group III., Secondary Remiges V.–VII.	Present Cubital Group I., Secondary Remiges VIII.–X. —Cubiti veri XI.–*x*.

Direction of Moult.

From the foregoing scheme it may be observed that there are no flight-feather equivalents allotted to the phalangeal portion of Digit I., in which part they figure as "suppressed."

Such a condition is quite conceivable and in perfect accord with suppression of quills in other portions, as, for instance, the reduction on the extreme phalanx of the second finger from 12 to 11 (Podicepidæ, Pelargi, &c.), and from 11 to 10 and 9 in Passeres (Gadow, 21, pp. 656 &c.). This tendency towards a part-suppression, if carried further, would have the effect of leading to total apoptilism. It, moreover, must have proceeded contemporaneously with the feathering of the forearm and was still in progress after, as is evidenced in the Passeres, where it has reached the present climax in the Oscines proper.

Considering the genealogical relative shortness of Digit I., coupled with the fact of a still greater reduction of size in the present forms of birds to one compound element, there is a strong probability existing that, during the course of the fusion of the phalangeal segments of this digit with its originally independent metacarpal bone,

they were stripped off one after the other as in the case of the "Remicle" and other diminutive terminal coverts. A likely procedure for feathers which at no time could have been of any considerable size, and certainly not more in number than three at the most.

The moult of the "Pennæ pollicis," moreover, synchronizing with that of Metacarpo-digitals VI.–X. and Cubitals I.–IV. (see Table VI.), is by no means an unimportant item for the argument that in their retrograde movement they were obstructed by the position which these latter, together with the "intercalaries" (as representing the metacarpal equivalents for Digit II.), had early taken up on the distal portion of the cubitus.

Finally, if the present inquiry into the moult of the individual bird, which, however, reflects all the phylogenetic conditions inherent to the Class as a whole (except perhaps the Spheniscidæ), has not thrown any further light upon the question as to whether "diastataxy" is due to either the hypothetical *absence* of a remex or the assumed *presence*, consequent upon the "shifting" process alone, as summarized by Pycraft (in his paragraph (1) p. 241, *l. c.*), it should at least have contributed materially towards the outstanding answer of the first part of the latter author's paragraph (3)—"The cause of this shifting is still a matter for investigation"; and also to the second part of the same sentence—"it is possibly due to a slight secondary lengthening of the forearm."

This latter interpretation does not seem to gather strength, especially when we perceive the ample manner in which the "moult" supplies the proof that "faulting" is not confined alone to diastataxic wings, but takes place, though in inferior degree, in the short-armed eutaxic forms of birds, such as the Passeres.

My sincere thanks are due to the following gentlemen:—

To Mr. J. Orme, of the Victorian Railways, Murchison East, Victoria, Australia, who by his disinterestedness in supplying me with the specimens has so materially aided me in my task.

To Dr. R. Bowdler Sharpe, of the British Museum (Nat. Hist.), for his interest shown in its progress and encouraging me in its completion.

To Dr. Chalmers Mitchell, F.Z.S., F.L.S., &c., for his valuable advice and suggestions made on the form of this memoir and its preparation for publication.

To C. Davies Sherborn, Esq., F.Z.S., for his generous act of revising the MS.

To the Editor, for the facilities given me in kindly placing at my disposal the use of the Library of the Zoological Society.

Also to the Staff of the Society's Library and the Publication Department, for the ever-courteous manner in which my wants were met.

X.—Bibliography.

(1) Allen, J. A.—"Alleged Changes of Colour in the Feathers of Birds without Moulting," Bull. Am. Mus. Nat. Hist. art. 3, vol. viii. 1896, pp. 13–42.

(2) Altum, B.—"Ueber den Bau der Federn als Grund ihrer Färbung, ein Beitrag zur Pterologie," Journ. für Ornithologie, ii. Jahrg. 1854, art. 1 (Erinnerungschrift), pp. xix–xxxv.

(3) Beddard, F. E., M.A., F.R.S.—'The Structure and Classification of Birds.' London, 1898 (Longman, Green, & Co.).

(4) Blyth, Edward.—"On the Reconciliation of certain apparent Discrepancies observable in the Mode in which the Seasonal and Progressive Changes of Colour are effected in the Fur of Mammalians and Feathers of Birds; with various Observations on Moulting," Magazine of Natural History (Charlesworth's), vol. i. (May 1837), art. 9, pp. 259–281; continued June 1837, art. 3, pp. 300–310.

(5) Böck, Prediger.—"Ausfallen der Mauser bei einem Vogel in der Gefangenschaft," Journ. f. Ornith. i. Jahrg. 1853, iii. Heft, No. 3, p. 267.

(6) Brehm, Chr. Ludwig.—"Bemerkungen über den Federnwechsel und das Sich-Ausfärben des Gefieders" (Bericht an die Ornithologen Versammlung zu Halberstadt), Journ. f. Ornith., Extraheft, i. Jahrg. 1853, Art. 3, pp. xxiv &c.

(7) Brehm, Chr. Ludwig.—"Die Mauser der jungen Raubvögel und der Uebergang ihres Jugendkleides in das Ausgefärbte," Journ. f. Ornith. i. Jahrg. 1853, iii. Heft, No. 3, pp. 196 &c.

(8) Brehm, Chr. Ludwig.—*Ibid.* Continuation, v. Heft, No. 5, pp. 343–346.

(9) Brehm, Chr. Ludwig.—"Gegen Schlegel's Meinung über die Verfärbung des Gefieders," *ibid.* p. 347.

(10) Brehm, Chr. Ludwig.—"Verfärbung und Federnwechsel der Europäischen Seeschwalben," *ibid.* ii. Jahrg. 1854, iv. Heft, No. 10, pp. 317–322.

(11) Chadbourne, Arthur P., M.D.—"The Spring Plumage of the Bobolink (*Dolichonyx oryzivorus*), with Remarks on the 'Colour-change' and 'Moulting,'" The Auk, vol. xiv. no. 2, April 1897, pp. 111–154.

(12) Chalmers Mitchell, P., M.A., F.Z.S., F.L.S.—"On so-called 'Quintocubitalism' in the Wing of Birds; with special reference to the Columbæ, and Notes on Anatomy," Journ. Linn. Soc. Lond., Zool. vol. xxvii. no. 175, July 1, 1899, pp. 210–236, pls. 12 & 13.

(13) Chapman, F. M.—"The Changes of Plumages in the Dunlin and Sanderling," Bull. Am. Mus. Nat. Hist. vol. viii. art. 1, 1896, pp. 1–8.

(14) Chapman, F. M.—"On the Changes of Plumage in the Snowflake (*Plectrophenax nivalis*)," *ibid.* art. 2, pp. 9 &c.

(15) Chapman, F. M.—"Remarks on the Spring Moult of the Bobolink," The Auk, vol. xiv. 1897, pp. 150–154.

(16) Degen, Edward.—"On some of the Main Features in the Evolution of the Bird's Wing," Bull. Brit. Orn. Club, vol. ii. 1894, pp. i–xxxiii, pl. i.

(17) Dwight, Jonathan.—"The Sequence of Plumages and Molts of the Passerine Birds of New York," Am. Ac. Sci. New York, vol. xiii. 1900, pp. 87 &c., with plates.

(18) Dwight, Jonathan, Jun., M.D.—"The Sequence of Molts and Plumages of the 'Laridæ' (Gulls and Terns)," The Auk, vol. xviii. Jan. 1901, no. 1, pp. 49–63.

(19) Fatio, Dr. Victor.—"Des Diverses Modifications dans les Formes et la Coloration des Plumes," Mém. Soc. Phys. d'Hist. Nat. Genève, tome xviii. 1866, pp. 250–295.

(20) Gadow, Dr. Hans.—"On the Colour of Feathers as affected by their Structure," Proc. Zool. Soc. Lond. 1882, pp. 409–421, pls. xxvii., xxviii.

(21) Gadow, Dr. Hans.—"Remarks on the Numbers and on the Phylogenetic Development of the Remiges of Birds," *ibid.* 1888, pp. 655–667, parts i. & ii.

(22) Gätke, H.—"Einige Beobachtungen über Federnwechsel durch Verfärbung ohne Mauser," Journ. f. Ornith. ii. Jahrg. 1854, iv. Heft, No. 10, pp. 321 &c.

(23) Gerbe, Z.—"Sur les Plumes du Vol et leur Mue," Bull. Soc. Zool. France, 1877, tome ii. pp. 289–290.

(24) Gloger, Dr. C. W. L.—"Bemerkungen über den Aufsatz Martin's," Journ. f. Ornith. i. Jahrg. 1853, i. Heft, No. 1, pp. 19–28.

(25) Gloger, Dr. C. W. L.—"Zur Erklärung der Verfärbung des Gefieders," *ibid.* iv. Heft, No. 4, pp. 269–275.

(26) Gloger, Dr. C. W. L.—"Sollten Kraniche wohl eine besondere Sommertracht haben?" *ibid.* iv. Jahrg. 1856, v. Heft, pp. 392–394.

(27) Goodchild, J. G., F.Z.S., F.G.S.—"Observations on the Disposition of the Cubital Coverts in Birds," Proc. Zool. Soc. Lond. 1886, pp. 184–203.

(28) Hesler, A.—"Ornithologische Beobachtungen," Journ. f. Ornith. ii. Jahrg. 1854, ii. Heft, No. 8, pp. 185 &c., 286.

(29) Holland, Theodor.—"Zur Entwickelungsgeschichte der Federn," Journ. f. Ornith. viii. Jahrg. 1860, v. Heft, No. 47, pp. 341–347; *ibid.* continuation, vi. Heft, No. 48, pp. 432–442, pl. i. figs. 1–11.

(30) Homeyer, E. von.—"Feder- und Farbenwechsel," *ibid.* iii. Jahrg. 1855, iv. Heft, No. 16, p. 347.

(30 *a*) Homeyer, E. von.—"Ein ferneres Wort über das Ausfärben," *ibid.* ii. Heft, No. 14, 1854, pp. 113–117.

(31) Homeyer, E. von.—"Noch ein Wort über die Verfärbung," *ibid.* iv. Jahrg. 1856, ii. Heft, No. 20, pp. 129–132.

(32) Martin, Leopold.—"Ueber den Farbenwechsel bei *Muscicapa collaris*, *M. atricapilla*, und *M. parva* im Frühlings," *ibid.* i. Jahrg. 1853, i. Heft, No. 1, pp. 16–18.
See also comment on this by Gloger (*ibid.* p. 19).

(33) Martin, Leopold.—"Zur Verfärbung des Gefieders, namentlich bei *Anas nigra*," *ibid.* iv. Heft, No. 4, pp. 208 &c.

(34) Meves, W.—"Ueber die Farbenveränderung der Vögel durch und ohne Mauser," *ibid.* iii. Jahrg. 1855, iii. Heft, No. 15, pp. 230 &c. Taf. ii. & iii.

(35) Millais, John Guille, F.Z.S.—"On the Change of Birds to Spring Plumage without a Moult," The Ibis, 7th ser. vol. ii. 1896, art. 40, pp. 451–457, pl. x.

(36) Müller, Dr. Baron v.—"Ueber den Farbenwechsel der Vögel," Journ. f. Ornith. i. Jahrg. 1853, v. Heft, No. 5, pp. 327–329.

(37) Nitzsch, Christian Ludwig.—"Pterylography." Translated by Ph. Lutley Sclater, M.A., Ph.D., F.R.S., for the Ray Society of London, 1867.

(38) Pycraft, W. P.—"A Contribution to the Pterylography of Birds' Wings," Trans. Leicester Lit. & Phil. Soc. vol. ii. part 3, April 1890, pp. 1–22.

(39) Pycraft, W. P., A.L.S.—"Some Facts concerning the so-called 'Aquintocubitalism' in the Bird's Wing," Journ. Linn. Soc. Lond., Zool. vol. xxvii. July 1, 1899, pp. 236–256, pls. 14–16.

(40) Schlegel, Dr. Hermann.—"Sendschreiben an die am 6ten Julius 1852 zu Altenburg versammelten Naturforscher," Naumannia, 1852, ii. Bd. ii. Heft, No. 1, pp. 19–24 &c.

(41) Schlegel, Dr. Hermann.—"Verfärbung das Gefieders," Journ. f. Ornith. i. Jahrg. 1858, i. Heft, No. 1, p. 67.

(42) Schlegel, Dr. Hermann.—"Ueber das Wachsthum nnd die Farbenveränderungen der Federn der Vögel," *ibid.* iii. Jahrg. 1855, ii. Heft, No. 19, p. 255.

(43) Sundevall, C. J.—"Ueber die Flügel der Vögel," *ibid.* ii. Jahrg. 1855, ii. Heft, No. 14, pp. 118–163.

(44) Wittmer Stone.—"The Molting of Birds, with special reference to the Plumages of the smaller Land-Birds of Eastern North America," Proc. Acad. Nat. Sc. Philadelphia, 1896, pp. 108–127.

(45) Wray, R. S., B.Sc.—"Note on a Vestigial Structure in the Adult Ostrich representing the Distal Phalanges of Digit III.," Proc. Zool. Soc. Lond. 1887, pp. 283 & 284, text-figures 1–4.

(46) Wray, R. S., B.Sc.—"On some Points in the Morphology of the Wings of Birds," *ibid.* pp. 343-355, pls. xxix.–xxxii.

XI.—EXPLANATION OF PLATES XXXVI.–XXXVIII.

The Roman figures placed at the head of each diagram denote the numerical order of the flight-feathers, as counted from the wrist-joint, outwards for the digital portion, inwards for the cubital portion of the left and right wing respectively.

The broader dark vertical bars indicate those remiges which are in progress of moult.

The symbol 0, placed over the bar indicated by dots only, signifies this particular remex is shed off.

The numbers placed immediately above the bars express the actual length of growth of the remex represented by that bar, in millimetres.

The proportionate growth of the remiges in moult may be read off on the scale from 0–100 (100 standing for full growth), which is provided for each diagram.

The small letters beneath each diagram indicate the chronological appearance of the remiges on the two portions of the wing—plain letters for the metacarpo-digital; with a dash, thus ′, for the cubital portion.

PLATE XXXVI.

PLATE XXXVI.

Diagram A. Showing moult of metacarpo-digital remiges I. and II., or *a* and *b*, also their corresponding equivalents VIII. and IX., or *a'*, *b'*, on the cubital portion.

Diagram B. Illustrates the anomalous case peculiar to the moult of metacarpo-digitals III., IV., and V., or *c*, *d*, and *e*, a triplet of remiges which has no corresponding equivalent on the cubital portion at this stage of development.

Diagram C. Stage of development of previous diagram in a more advanced condition of moult, besides which remex VI. or *f*, or the next in turn, is shown.

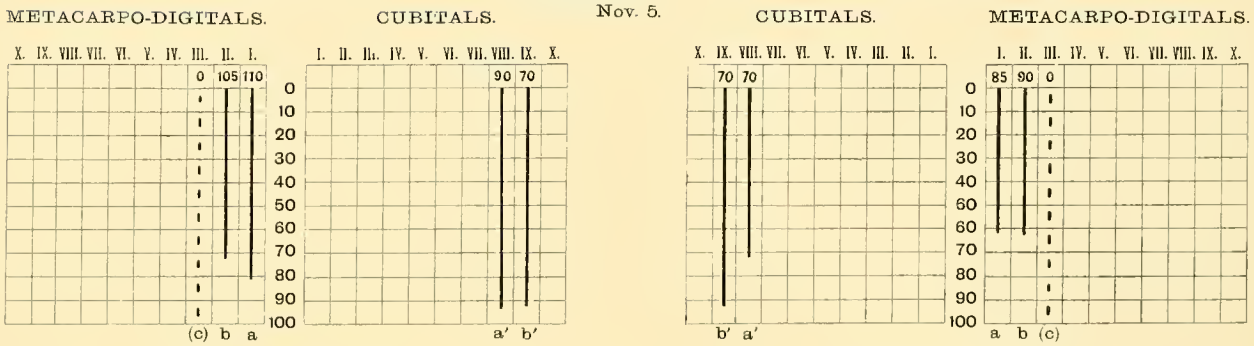
On the cubital portion of the left side are seen also the remiges I., X., and VII., lettered f', f'', and f''' respectively, the triplet of flight-feathers which restores the temporary asymmetry formed by *c*, *d*, and *e* on the hand-portion, as shown in diagram B.

Diagram D. Showing moult of metacarpo-digital VII., or *g*. The moult of its corresponding remex II., or g', is indicated at this stage by being shed off. This stage forms one of transition between f, f', f'', f''' to that of g, g'.

Left Side Wing. Right Side Wing.

SPECIMEN No. 1. ad. ♂ Nov. 5.

A

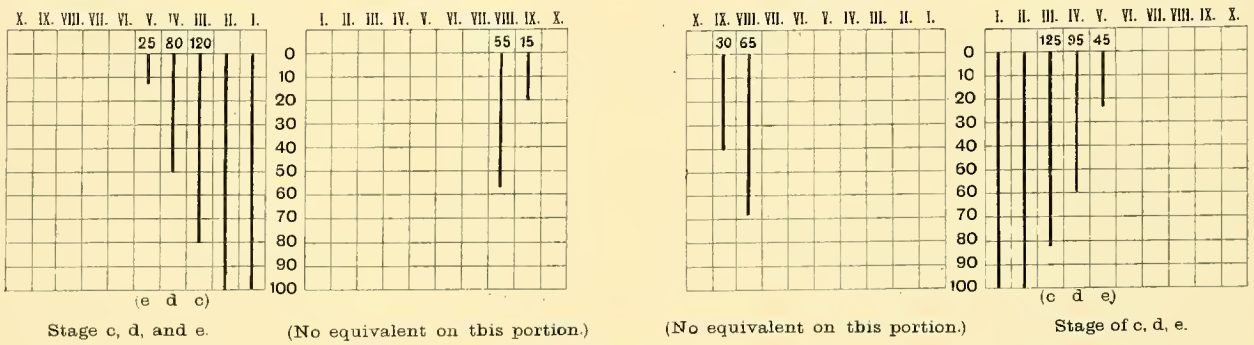


Stage of a and b, and a′, b′.

Stage of a, b, and a′, b′.

SPECIMEN No. 3. juv. ♀ Nov. 14.

B



Stage c, d, and e.

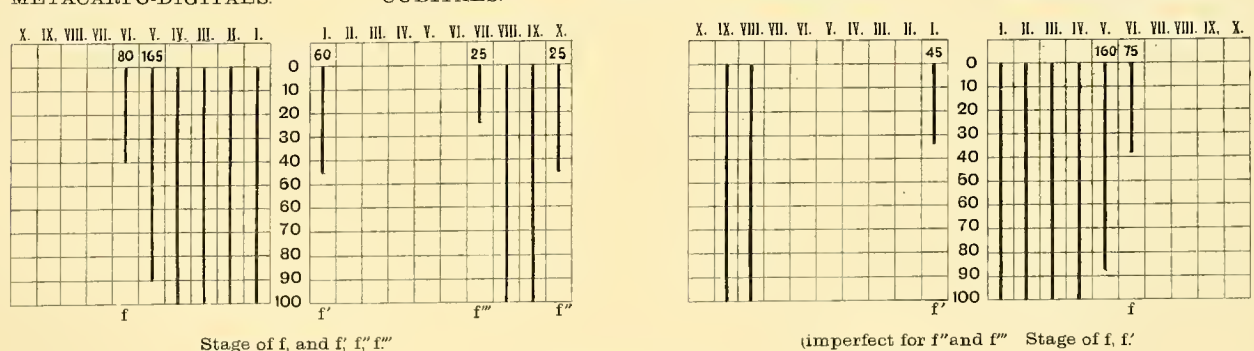
(No equivalent on this portion.)

(No equivalent on this portion.)

Stage of c, d, e.

SPECIMEN No. 7. ad. ♂ Nov. 19.

C



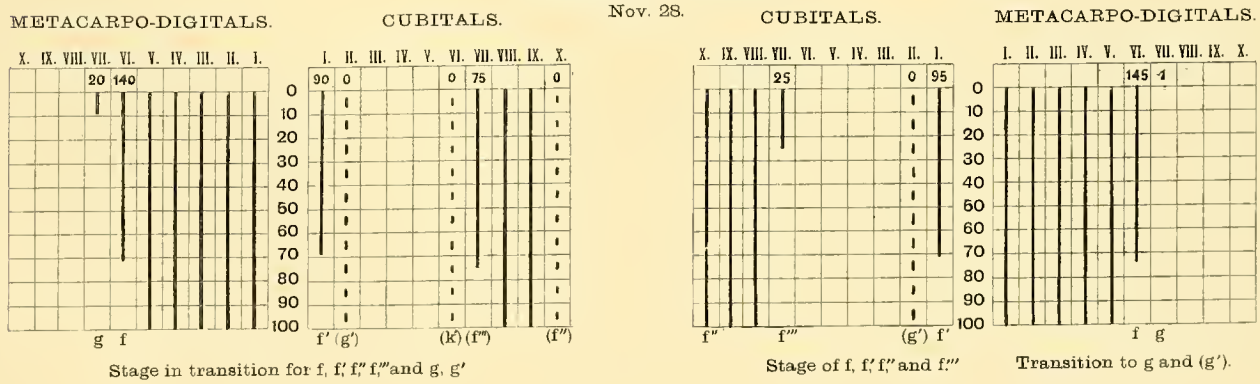
Stage of f, and f′, f″, f‴.

(imperfect for f″ and f‴ see left side wing.)

Stage of f, f′.

SPECIMEN No. 10. ad. ♂ Nov. 28.

D



Stage in transition for f, f′, f″, f‴ and g, g′

Stage of f, f′, f″ and f‴

Transition to g and (g′).

E Degen, del

Bale & Danielsson, Ltd

DIAGRAMS ILLUSTRATING THE MOULT OF THE REMIGES IN GYMNORHINA TIBICEN.

PLATE XXXVII.

PLATE XXXVII.

DIAGRAM E. Stage for moult of metacarpo-digital VII., or *g*, and cubital remex II., or *g'*, repeated. Here the conditions are reversed to those of diagram D. In this specimen it is the hand-portion which is in arrear, while the cubital portion is in advance.

DIAGRAM F. Intermediate phase of moult for metacarpo-digital remex VIII., or *h* (in arrear on both wings in this specimen), and its equivalent on the cubital portion remex III., or *h'*. This forms a case of transition from *g* to *h*.

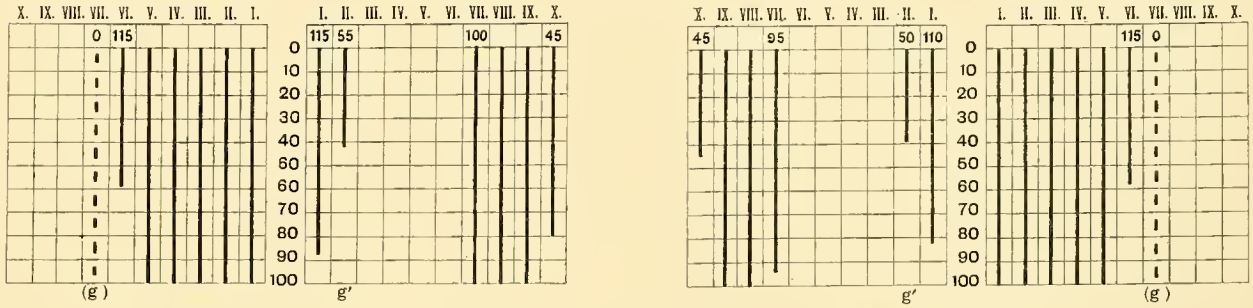
DIAGRAM G. Showing stage of moult for *h*, hand-portion, and *h'*, cubital portion, in perfectly normal condition. Also early indication for the moult of metacarpo-digital IX., or *i*, the next stage, on the left-side wing.

DIAGRAM H. Shows the moult for metacarpo-digital remex IX., or *i* (abnormally in arrear in this specimen), and its equivalent remex IV., or *i'*, on the cubitus. Stage of transition from *h* to *i*.

Left Side Wing. Right Side Wing.

SPECIMEN No. 11. juv.♀ Dec. 3.

E

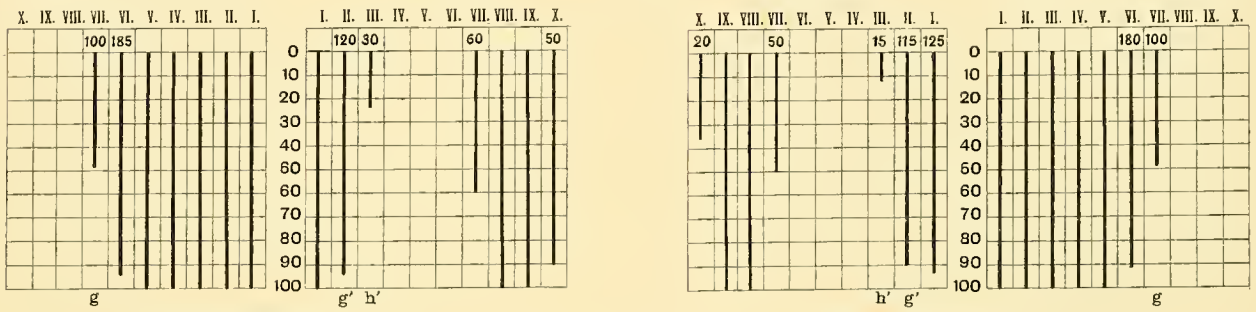


Stage supplementing development of g, g'.

Stage of g, g' supplemented.

SPECIMEN No. 16. juv.♂ Dec. 19.

F

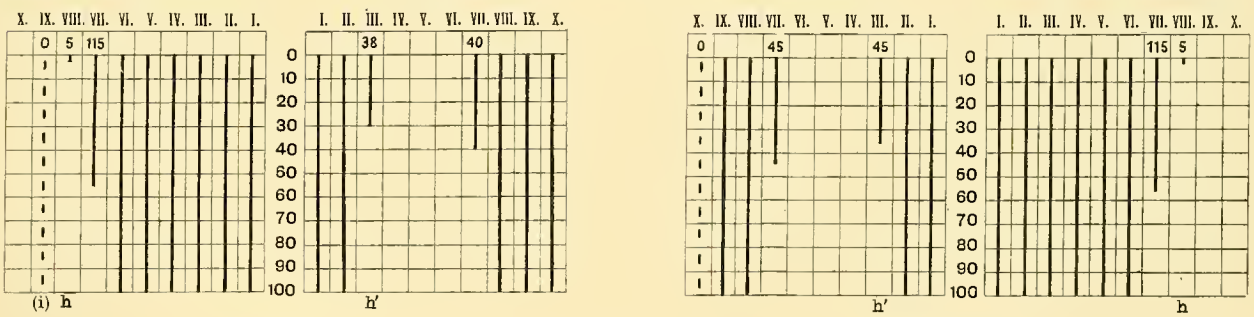


Stage of transition from g. to (h) h'.

Transition from stage g. g' to (h) h'

SPECIMEN No. 14. juv.♀ Dec. 11.

G

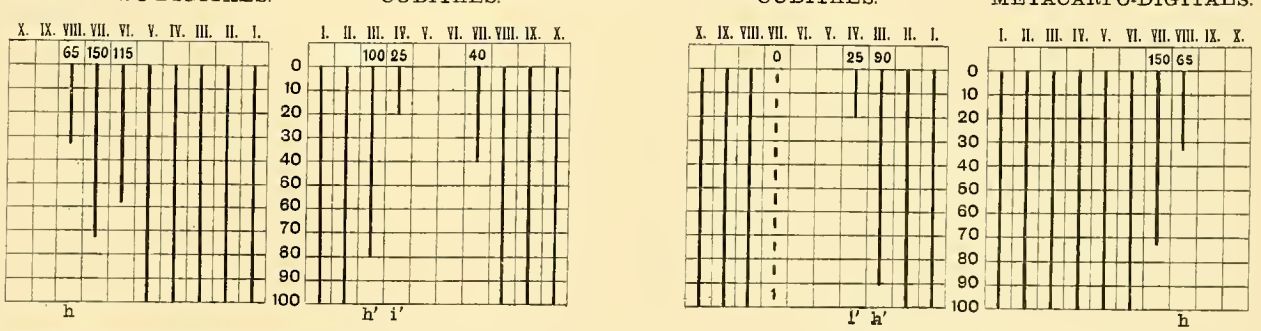


Stage of h, h'.

Stage of h, h'.

SPECIMEN No. 17. ad.♂ Jan. 1.

H



Stage of transition for development of h, h' and (i) in part i'.

Transition from stage h, h', to (i) i.'

E Degen, del

Bale & Danielsson. Ltd

DIAGRAMS ILLUSTRATING THE MOULT OF THE REMIGES IN GYMNORHINA TIBICEN.

PLATE XXXVIII.

PLATE XXXVIII.

Diagram J. Moult of remex IX., or *i*, on the hand-portion, and its corresponding remex IV. for the cubital portion, in a perfectly normal condition for the left-side, imperfect for the right-side wing.

Diagram K. Represents the stage for the development of metacarpo-digital X., or *k*, and that of its equivalent for the cubital remex VI., or *k'*.

Diagram L. Shows the final stage of the moult for the flight-feathers, or that of cubital remex V., and lettered *l'*, which under normal conditions finds no equivalent on the hand-portion. It further supplements stage *k*, *k'* for the left-side wing only, being in arrear of moult for these on the right side.

Diagram M. Specimen in arrear for the moult of metacarpo-digital X. on both sides, but otherwise showing final stage, or that of cubital V., to advantage.

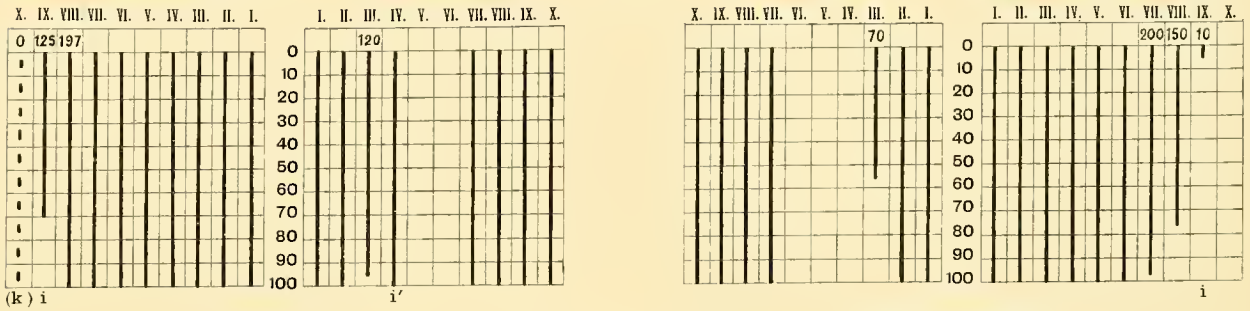
Left Side Wing.

Right Side Wing.

SPECIMEN No. 21. ad. ♂
Jan. 29.

J

METACARPO-DIGITALS. CUBITALS. CUBITALS. METACARPO-DIGITALS.



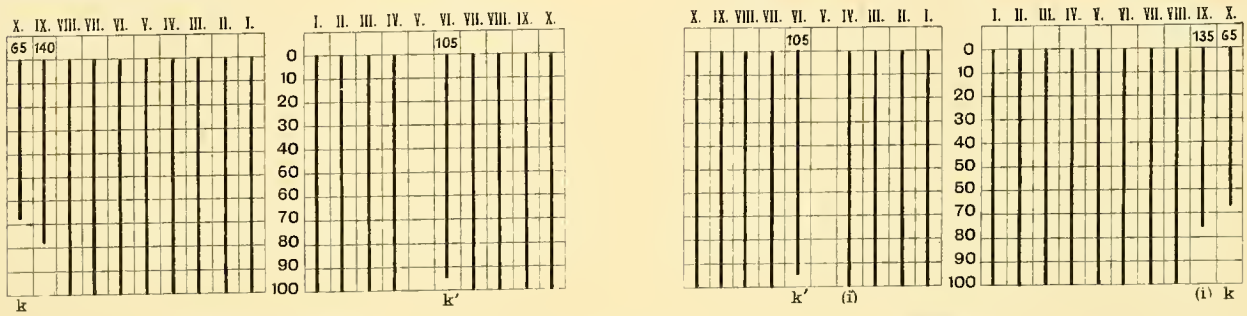
Stage of i and i'.

Stage of i (imperfect for i').

SPECIMEN No. 25. ad. ♂
Feb 18.

K

METACARPO-DIGITALS. CUBITALS. CUBITALS. METACARPO-DIGITALS.



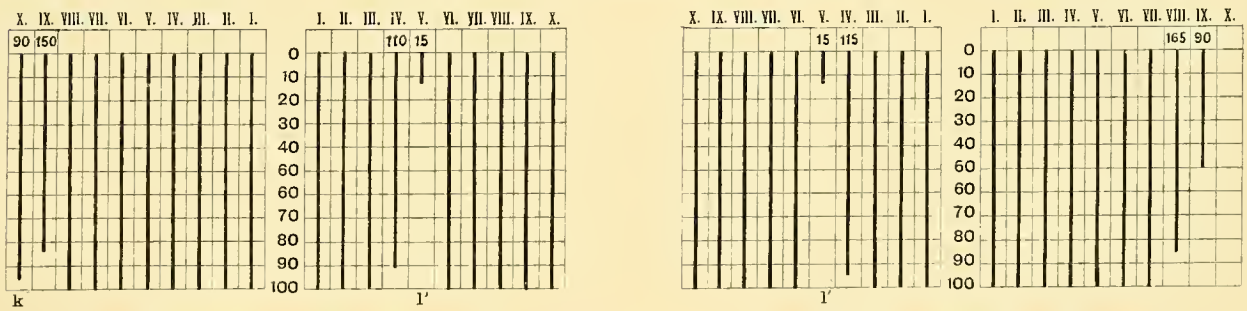
Stage of k and k'.

Stage of k, k'.

SPECIMEN No. 26. ad ♂
March 4.

L

METACARPO-DIGITALS. CUBITALS. CUBITALS. METACARPO-DIGITALS.



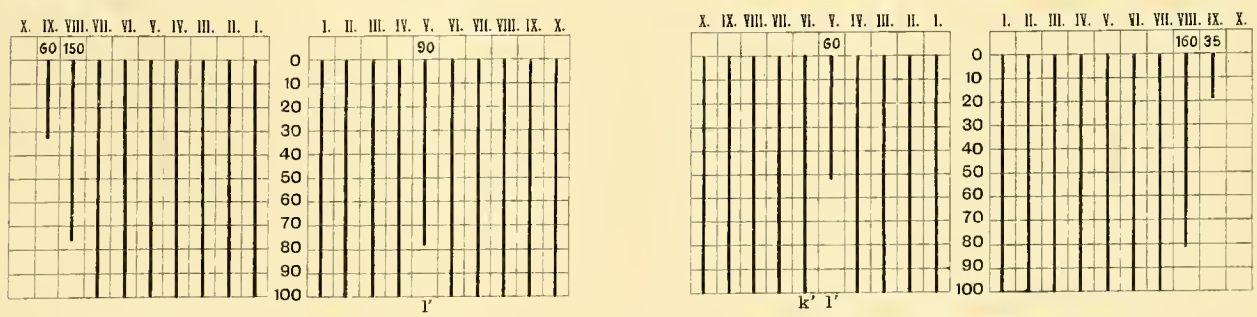
Stage of l' (no equivalent on hand portion).

Stage of l' (no equivalent on hand portion).

SPECIMEN No. 24. ad. ♂
Feb. 18.

M

METACARPO-DIGITALS. CUBITALS. CUBITALS. METACARPO-DIGITALS.



Supplementary stage of l' (final development) spec. in arrear for k, complete for k'.

Stage of l' (further development) in arrear for k complete for k'.

E Degen, del

Bale & Danielsson, L^td

DIAGRAMS ILLUSTRATING THE MOULT OF THE REMIGES IN GYMNORHINA TIBICEN.

LIST OF THE PAPERS CONTAINED IN VOL. XVI.

Page

Beddard, Frank E., M.A., F.R.S., Prosector and Vice-Secretary of the Society.
Contribution towards a Knowledge of the Osteology of the Pigmy Whale (*Neobalæna marginata*) 87

Boulenger, G. A., F.R.S., F.Z.S.
Third Contribution to the Ichthyology of Lake Tanganyika.—Report on the Collection of Fishes made by Mr. J. E. S. Moore in Lakes Tanganyika and Kivu during his Second Expedition, 1899–1900 137

Brady, George Stewardson, M.D., LL.D., D.Sc., F.R.S., C.M.Z.S.
On new or imperfectly-known Ostracoda, chiefly from a Collection in the Zoological Museum, Copenhagen 179

Budgett, J. S., M.A., F.Z.S., Trinity College, Cambridge.
On the Breeding-habits of some West-African Fishes, with an Account of the External Features in Development of *Protopterus annectens*, and a Description of the Larva of *Polypterus lapradei* .. 115
On the Structure of the Larval *Polypterus* 315

Degen, Edward, F.Z.S.
Ecdysis, as Morphological Evidence of the Original Tetradactyle Feathering of the Bird's Fore-limb, based especially on the Perennial Moult in *Gymnorhina tibicen* 347

Page

Howes, G. B., LL.D., F.R.S., and Swinnerton, H. H., B.Sc., Marshall Scholar, R. Coll. Sci. Lond.
On the Development of the Skeleton of the Tuatara, *Sphenodon punctatus*; with Remarks on the Egg, on the Hatching, and on the Hatched Young. (From the Huxley Research Laboratory.) 1

Lankester, E. Ray, M.A., LL.D., F.R.S., F.Z.S., Director of the Natural History Departments of the British Museum, Correspondent of the Institute of France.
On *Okapia*, a new Genus of *Giraffidæ*, from Central Africa 279

Mudge, Geo. P., A.R.C.S. Lond., F.Z.S., Lecturer on Biology, London School of Medicine for Women, and Demonstrator of Biology, London Hospital Medical School.
On the Myology of the Tongue of Parrots, with a Classification of the Order, based upon the Structure of the Tongue 211

Swinnerton, H. H., B.Sc., Marshall Scholar, R. Coll. Sci. Lond., and Howes, G. B., LL.D., F.R.S.
On the Development of the Skeleton of the Tuatara, *Sphenodon punctatus*; with Remarks on the Egg, on the Hatching, and on the Hatched Young. (From the Huxley Research Laboratory.) 1

INDEX OF SPECIES, ETC., IN VOL. XVI.

Acanthias, 50.
Acerina, 156.
Acipenser, 51, 332.
Acrosaurus, 3.
Africa, on the Breeding-habits of some Fishes of West, 115–136.
Agama, 73.
Aipysurus annulatus, 3.
Alces, 285, 286, 287.
Alestes lemairii, 137.
—— *macrolepidotus*, 140, 143.
—— *macrophthalmus*, 137, 140, 143.
Amia, 327, 330, 337, 338.
Amphioxus, 51.
Anas nigra, 411.
Anchitherium, 289.
Anoplopterus platychir, 140.
Anser, 261.
Antilocapra, 287, 296, 297.
Aprosmictus, 258, 259.
Apteryx, 33.
Ara, 212, 226, 234, 249, 251, 255, 262, 263, 264.
—— *ararauna*, 215, 219, 227, 229, 240, 245, 247, 253, 255, 259, 260, 261, 268, 276.
—— *macao*, 211, 213, 219, 220, 221, 222, 224, 227, 229, 240, 245, 255, 259, 261, 268, 274, 276.
Archæopteryx, 2.
Armadillo, 292, 296.
Ascahabotes fasciculatus, 50.
Asprotilapia leptura, 141, 159, 178.
Asterope sp., 199.
—— *brevis*, 183.
—— *lichenoides*, 180, 206.
—— *oculata*, 179, 202.
—— *quadrata*, 180.
Auchenoglanis biscutatus, 137, 140, 148.
Bairdia hirsuta, 197.
—— *longisetosa*, 197, 210.
—— *villosa*, 197.
Balæna, 87, 89, 91, 93, 94, 95, 99, 101, 102, 103, 104, 105, 106, 107.
—— *australis*, 94, 95, 96, 98, 101.
—— *marginata*, 88, 89.
—— *mysticetus*, 98, 101.
—— (*Caperea*) *antipodarum*, 89.
Balænoptera, 90, 93, 94, 95, 96, 99, 101, 102, 103, 104, 105, 106, 107.
—— *huttoni*, 95, 96.
—— *laticeps*, 94.
—— *musculus*, 93, 95, 96, 98, 107.
—— *rostrata*, 92, 94, 95, 96, 99, 104, 107.
—— *sibbaldi*, 94, 96, 99, 104.
Barbus altianalis, 140, 144, 145, 164.
—— *capensis*, 144.
—— *kessleri*, 145.
—— *mariquensis*, 145.
—— *platyrhinus*, 140, 144, 162.
—— *serrifer*, 140, 145, 166.
—— *tropidolepis*, 140, 145, 164.
Barilius moorii, 140, 146, 166.
—— *tanganicæ*, 140, 146, 166.
—— (*Pelotrophus*) *microlepis*, 147.
Barita destructor, 396.
—— *strepera*, 396.
—— *varia*, 396.
Bathybates fasciatus, 141, 153, 172.
—— *ferox*, 141, 153.
Beddard, F. E. Contribution towards a Knowledge of the Osteology of the Pigmy Whale (*Neobalæna marginata*), 87–114.
Bolborhynchus, 222, 223, 226, 227, 234, 245, 249, 253, 254, 255, 256, 259, 261, 262, 263, 266.
—— *lineolatus*, 222, 231, 242, 278.

Boulenger, G. A. Third Contribution to the Ichthyology of Lake Tanganyika.—Report on the Collection of Fishes made by Mr. J. E. S. Moore in Lakes Tanganyika and Kivu during his Second Expedition, 1899–1900, 137–178.

Brady, G. S. On new or imperfectly-known Ostracoda, chiefly from a Collection in the Zoological Museum, Copenhagen, 179–210.

Bramatherium, 292, 293, 296.

Brotogerys, 221, 222, 223, 225, 226, 234, 238, 239, 242, 245, 249, 252, 253, 254, 259, 261, 262, 263, 268.

—— *pyrrhopterus*, 221, 238, 252, 276.

Buceros, 397.

Budgett, J. S. On the Breeding-habits of some West-African Fishes, with an Account of the External Features in Development of *Protopterus annectens*, and a Description of the Larva of *Polypterus lapradei*, 115–136.

——. On the Structure of the Larval *Polypterus*, 315–346.

Cacatua, 214, 217, 219, 227, 233, 249, 253, 254, 255, 262, 263.

—— *alba*, 214, 215, 219, 226, 227, 232, 233, 237, 243, 245, 258, 263, 268.

—— *galerita*, 214, 215, 216, 217, 220, 221, 226, 227, 228, 229, 232, 235, 245, 253, 258, 259, 261, 262, 263, 268, 272, 274, 276.

—— *leadbeateri*, 217, 218, 223, 224, 226, 227, 232, 235, 242, 245, 249, 261, 263, 268.

—— *roseicapilla*, 215, 226, 227, 228, 232, 235, 242, 245, 249, 253, 258, 261, 263, 268, 351.

—— *sulphurea*, 214, 218, 226, 227, 233, 237, 253, 254, 258, 261, 268.

—— *triton*, 214, 219, 226, 227, 233, 237, 240, 243, 245, 258, 263, 268.

Caica, 226, 227, 234, 243, 245, 249, 253, 254, 261, 263, 264, 266.

—— *leucogaster*, 224, 231, 242.

Calamoichthys, 317, 320, 327, 328, 332.

Calopsittacus, 226, 227, 235, 245, 250, 251, 253, 256, 259, 261, 262, 263, 268.

—— *novæ-hollandiæ*, 218, 227, 233, 249.

Calyptorhynchus, 217, 227, 243, 245, 249, 250, 253, 254, 261, 262, 263.

—— *banksii*, 215, 226, 227, 228, 232, 237, 254, 268.

Calyptorhynchus funereus, 215, 226, 227, 232, 237, 253, 259, 268.

Candonella virescens, 193, 210.

Candonopsis complanata, 196, 210.

Caperea antipodarum, 89.

Capoëta dilloni, 144.

—— *fundulus*, 144.

—— *tanganicæ*, 140, 143, 144, 162.

—— *trutta*, 144.

Capra, 287.

—— *ægagrus*, 302.

Ceratodus, 328.

Certhiola, 212.

Ceryle alcyon, 390.

Chamæleo, 30.

Champsosaurus, 3.

Chauna, 261.

Chelone mydas, 57.

Chenopis atrata, 366.

Chitra, 70.

Chlamydoselache, 329.

Chromis tanganicæ, 158.

Chrysichthys brachynema, 140, 148, 168.

—— *cranchii*, 140, 147, 148.

—— *myriodon*, 140, 147.

—— *sharpii*, 137.

Chrysotis, 212, 213, 234, 249, 250, 252, 253, 254, 255, 256, 262, 263.

—— *æstiva*, 219, 226, 230, 235, 245, 253, 259, 261, 268.

—— *leucocephala*, 211.

—— *ochrocephala*, 219, 220, 226, 227, 229, 230, 235, 236, 245, 249, 259, 261, 268, 274, 276.

—— *panamensis*, 219, 226, 227, 230, 235, 236, 245, 261, 268, 274.

—— *viridigena*, 219, 226, 227, 236, 239, 245, 258, 259, 268.

—— (*viridigenalis*) *viridigena*, 229.

Cichla, 156.

Ciconia, 261.

Citharinus gibbosus, 140, 143.

Clarias liocephalus, 140.

—— *robecchii*, 140.

Codonocera, gen. nov., 188.

—— *cruenta*, 188, 204.

Colius, 397.

Columba domestica, 360.

Conchœcia hyalophyllum, 199.
—— *magna*, 199.
—— *maxima*, 199.
—— *porrecta*, 199.
—— *spinirostris*, 190, 199.
—— *striata*, 190, 199.
Conchœcilla lacerta, 199.
Conchœcissa cucullata, 179, 191, 199, 208.
—— *imbricata*, 199.
Conurus, 234, 249, 250, 252, 263.
—— *cactorum*, 220, 226, 227, 230, 234, 238, 239, 242, 245, 253, 254, 255, 262, 268, 276.
—— *carolinensis*, 212, 270.
—— *holochlorus*, 220, 226, 227, 230, 234, 236, 240, 242, 244, 245, 250, 253, 254, 259, 262, 263, 266.
—— *jendaya*, 220, 226, 227, 230, 231, 234, 238, 239, 245, 248, 253, 254, 255, 259, 261, 262, 266, 272, 276.
Coracopsis, 221, 226, 227, 234, 236, 241, 242, 243, 244, 245, 249, 253, 254, 258, 262, 264, 268.
—— *vasa*, 220, 227, 236, 274, 276.
Corvus, 261.
Cyanolyseus, 226, 227, 234, 239, 245, 249, 252, 253, 261, 262, 263.
—— *patagonicus*, 219, 230, 234, 239, 268.
Cyanorhamphus, 226, 227, 234, 243, 245, 249, 251, 254, 255, 261, 262, 263, 264, 266.
—— *auriceps*, 224, 231, 242.
Cyclasterope brevis, 183, 208.
—— *fascigera*, 181, 202.
—— *similis*, 183, 206.
Cygnus, 261.
Cypretta sarsi, 195, 210.
Cypridina foveolata, 184, 204.
—— *granulosa*, 184, 202.
—— *insolita*, 184, 204.
Cypridinodes, gen. nov., 187.
—— *favus*, 187, 204.
Cypridopsis aculeata, 193.
—— *marmorata*, 193, 206.
—— *minna*, 195.
Cyprinotus dentato-marginatus, 196, 206.
—— *fragilis*, 196, 206, 210.
—— *prasina*, 196.
Cypris flexilis, 192, 206.
—— *lætevirens*, 193, 206.
Cypris virens, 192, 206.
Cythere lutea, 198.
—— *rubida*, 198.
—— *sicula*, 198, 210.
Dacelo gigas, 391.
Degen, E. Ecdysis, as Morphological Evidence of the Original Tetradactyle Feathering of the Bird's Fore-limb, based especially on the Perennial Moult in *Gymnorhina tibicen*, 347–412.
Deroptyus, 226, 227, 234, 244, 245, 246, 263, 264, 266.
—— *accipitrinus*, 220, 229, 240, 242.
Dinoceras, 282.
Dipsosaurus, 23.
Dolichonyx oryzivorus, 352, 410.
Dolichosoma longissimum, 323.
Dromæus, 261.
Ecdysis, as Morphological Evidence of the Original Tetradactyle Feathering of the Bird's Fore-limb, 347–412.
Eclectus, 226, 227, 231, 233, 245, 249, 250, 252, 253, 254, 255, 258, 259, 261, 262, 263, 268.
—— *pectoralis*, 220, 230, 231, 233, 235, 278.
Ectodus descampsii, 141.
—— *longianalis*, 141, 154, 176.
—— *melanogenys*, 141.
Emydura, 62.
Eos, 222, 226, 227, 243, 247, 249, 252, 253, 254, 255, 257, 258, 259, 261, 262, 263.
—— *reticulata*, 213.
—— *riciniata*, 226, 232, 234, 242, 245, 266, 272, 278.
Equus johnstoni, 281, 282, 303.
Eretmodus cyanostictus, 141.
Eubalæna antipodarum, 89.
Euchonchœcia chierchiæ, 190, 208.
Eupathistona natans, 185, 186.
Fishes, on the Breeding-habits of some West-African, 115–136.
—— of Lakes Tanganyika and Kivu, Report on Mr. J. E. S. Moore's Collections of, 137–178.
Galeopithecus, 289.
Galesaurus, 3.
Gallinula chloropus, 404.
Gecko verticillatus, 71.
Gephyrochromis moorii, 141, 156, 178.

Giraffa, 285, 287, 288, 289, 290, 291, 292, 293, 294, 295, 296, 297, 300, 303, 305, 307.
Giraffidæ, on the new Genus *Okapia* of the Family, 279–314.
Globicephalus, 90.
Glossopsittacus concinnus, 407.
Glyptodon, 292, 296.
Gnathonemus stanleyanus, 137.
Grammatotria lemairii, 141.
Gymnarchus niloticus, Nesting-habits of, 115, 126, 131, 132, 136.
Gymnorhina leuconota, 403.
—— *tibicen*, on the Moult in, 347–412.
Haplochilus tanganicanus, 140.
Haplodactylus, 18.
Hatteria punctata, 71, 72, 73, 74.
—— (*Sphenodon*) *punctatus*, 74.
Helladotherium, 282, 285, 294, 300, 303.
Heptanchus, 329.
Heterodesmus, 188.
Heterotis niloticus, Nesting-habits of, 115, 128, 132, 136
Homœosaurus, 72.
Howes, G. B., and Swinnerton, H. H. On the Development of the Skeleton of the Tuatara, *Sphenodon punctatus*; with Remarks on the Egg, on the Hatching, and on the Hatched Young, 1–86.
Hydrocyon lineatus, 137, 140.
Hyloplesion, 52.
Hyperodapedon, 4, 36.
Hyperopisus bebe, Nesting-habits of, 115, 130, 131, 132, 136.
Ichthyology of Lake Tanganyika, Third Contribution to the, 137–178.
Ichthyophis, 44, 50, 332.
—— *glutinosa*, 46.
Iguana, 57.
Julidochromis ornatus, 141.
Kadaliosaurus, 36.
Kivu (Lake), on Mr. J. E. S. Moore's Collection of Fishes from, 137–178.
Kobus ellipsiprymnus, 287.
Lacerta, 41, 51, 57, 58.
—— *agilis*, 25.
—— *ocellata*, 25.
—— *viridis*, 7.
Lamprologus brevis, 140.
—— *compressiceps*, 140.
—— *elongatus*, 140.
—— *fasciatus*, 140.
—— *furcifer*, 140, 150.
—— *hecqui*, 140.
—— *lemairii*, 140, 150.
—— *modestus*, 140.
—— *moorii*, 140.
—— *tetracanthus*, 140.
—— *tretocephalus*, 140.
Lanius procerus, 396.
—— *undulatus*, 396.
Lankester, E. R. On *Okapia*, a new Genus of *Giraffidæ* from Central Africa, 279–314.
Lates microlepis, 140, 149.
Lathamus, 270.
Lepidosiren, 121, 122, 123, 124, 125, 126.
Lepidosteus, 321, 324, 327, 332, 334, 335, 336, 337.
Lomvia troile, 406, 407.
Lophophorus, 261.
Loriculus, 224, 226, 227, 245, 249, 253, 254, 255, 259, 261, 262, 263, 264, 266.
—— *galgulus*, 224, 230, 234, 240, 274, 278.
Lorius, 226, 242, 243, 246, 247, 249, 250, 254, 255, 257, 258, 261, 263, 264.
—— *domicella*, 213, 225, 227, 232, 234, 245, 247, 251, 254, 258, 259, 262, 266, 274, 278.
—— *flavo-palliatus*, 213, 224, 225, 226, 227, 232, 234, 245, 252, 254, 256, 258, 259, 262, 266, 278.
Malopterurus electricus, 140, 149.
Mastacembelus ellipsifer, 141.
—— *frenatus*, 141, 158, 178.
—— *moorii*, 141.
—— *ophidium*, 141.
—— *tæniatus*, 141, 160, 178.
—— *tanganicæ*, 141.
Megaptera, 96, 98, 99, 105.
Melopsittacus, 405.
Microconchœcia clausii, 199.
Microglossus, 226, 227, 235, 245, 249, 253, 258, 262, 263, 264, 268.
—— *aterrimus*, 213, 219, 229, 233.
Moore, J. E. S., on the Fishes collected in Lakes Tanganyika and Kivu by, 137–178.

Mormyrus longirostris, 137.
Mosasaurus, 14.
Moult of *Gymnorhina tibicen*, 347, 412.
Mudge, G. P. On the Myology of the Tongue of Parrots, with a Classification of the Order, based upon the Structure of the Tongue, 211–278.
Muscicapa atricapilla, 411.
—— *collaris*, 411.
—— *parva*, 411.
Mylodon, 296.
Myology of the Tongue of Parrots, Mudge on the, 211–278.
Nasiterna, 221, 226, 237, 243, 245, 249, 251, 253, 254, 259, 261, 262, 263, 264.
—— *pusio*, 218, 230, 233, 268, 278.
Nectarinia, 261.
Necturus, 50.
Neobalæna marginata, Osteology of, 87–114.
Nestor, 226, 227, 245, 247, 249, 250, 253, 254, 255, 257, 259, 262, 263, 270.
—— *notabilis*, 224, 232, 233, 235, 262, 266, 274, 278.
Nymphicus, 226, 227, 234, 243, 245, 255, 266.
—— *uvæensis*, 224, 227, 241.
Okapia, 279–314.
—— *johnstoni*, 288, 302, 303, 310.
Opisthocomus, 261.
Osteology of the Pigmy Whale, 87–114.
Ostracoda, on new or imperfectly-known, 179–210.
Otis, 261.
Palæohatteria, 22, 26, 30, 36, 52, 68.
Palæornis, 220, 226, 227, 231, 234, 240, 249, 251, 253, 254, 255, 259, 261, 262, 263.
—— *torquata*, 220, 231, 240, 250, 268, 272, 276.
Palæotragus, 288, 296, 303.
Palamedea, 261.
—— *cornuta*, 270.
Paraconchœcia gracilis, 199.
—— *inermis*, 199.
—— *oblonga*, 199.
—— *spinifera*, 199.
Paratilapia aurita, 141, 150, 176.
—— *bloyeti*, 138, 141, 151.
—— *calliura*, 141, 151, 176.
—— *dewindti*, 141.
—— *furcifer*, 141.
—— *leptosoma*, 141, 152.
Paratilapia macrocephala, 137.
—— *macrops*, 141.
—— *moeruensis*, 137.
—— *nigripinnis*, 141, 152, 176.
—— *pfefferi*, 141.
—— *stenosoma*, 141, 151, 172.
—— *ventralis*, 141.
—— *vittata*, 141, 150, 174.
Pariasaurus, 3, 69.
Parrots, Mudge on the Myology of the Tongue of, 211–278.
Pelecanus, 261.
Pelmatochromis lateralis, 154.
—— *polylepis*, 141, 153.
Peloneustes, 2.
Perca, 156.
Perissodus microlepis, 141.
Perissoglossa, 212.
Petrochromis polyodon, 141, 158.
—— *tanganicæ*, 141, 158.
Pezoporus, 221, 225, 226, 227, 234, 245, 249, 251, 253, 254, 255, 257, 258, 259, 261, 262, 263, 264, 266.
—— *formosus*, 222, 223, 231, 242, 272, 278.
Philomedes debilis, 186, 202.
—— *sculpta*, 182.
—— *sordida*, 186, 208.
Phrynocephalus, 30.
Phyllodactylus, 18.
Physalus antarcticus, 88.
—— *latirostris*, 99.
Pionopsittacus, 226, 227, 234, 245, 249, 253, 255, 261, 262, 264, 266.
—— *pileatus*, 230, 234, 240, 278.
Platycercus, 221, 222, 226, 227, 234, 242, 243, 245, 249, 251, 254, 255, 259, 261, 262, 263, 266.
—— *eximius*, 221, 231, 241, 272, 278, 351, 360, 382, 407.
Platydactylus, 51.
Plecodus paradoxus, 141.
Plectrophenax nivalis, 390, 410.
Plesiosaurus dolichodirus, 2.
Pleurodira, 62.
Pœocephalus, 231, 237, 242, 244, 249, 251, 254, 255, 259, 262, 263, 264.
—— *robustus*, 222, 226, 227, 231, 233, 241, 245, 249, 254, 261, 263, 266.

Percocephalus rüppelli, 221, 222, 226, 227, 231, 233, 237, 241, 245, 254, 261, 262, 266, 272.
Polypterus, Results of the Search for Eggs of, 115, 116.
——, on the Structure of the Larval, 315–346.
—— *bichir*, 142.
—— *congicus*, 140, 142.
—— *lapradii*, 317.
—— ——, Description of the Larva of, 115–136.
—— *senegalus*, 116, 117, 119, 317.
Prioniturus, 226, 227, 234, 245, 249, 251, 254, 256, 259, 260, 261, 262, 263, 264, 266.
—— sp., 222, 231, 242.
Pristiurus, 50.
Procellaria, 261.
Procolophon, 3.
Proterosaurus, 36.
Protopterus, the Habits and Life-history of, 115, 119.
—— *æthiopicus*, 140.
—— *annectens*, an Account of the External Features in Development of, 115–136.
Psephotus, 226, 227, 234, 249, 251, 254, 255, 261, 262, 264, 266.
—— *xanthorrhous*, 220, 227, 242.
Pseudopus, 14.
Psittacula, 226, 227, 234, 245, 249, 253, 254, 259, 261, 262, 263, 266.
—— *passerina*, 224, 231, 242, 278.
Psittacus, 212, 213, 220, 222, 226, 227, 234, 236, 237, 243, 244, 245, 249, 251, 253, 254, 258, 259, 261, 262, 263, 264, 268.
—— *erithacus*, 220, 230, 272, 274, 276.
—— *leucocephalus*, 212, 213.
—— *macao*, 211.
Psittinus, 222, 225, 226, 227, 230, 245, 249, 250, 252, 254, 261, 262, 263, 266.
—— *incertus*, 221, 222, 228, 240, 276.
Ptistes, 226, 227, 234, 237, 240, 241, 245, 249, 251, 253, 254, 258, 259, 261, 262, 263, 264, 266.
—— *erythropterus*, 217, 223, 231, 240, 272, 276.
Pyrocypris americana, 185, 202.
—— *chierchiæ*, 185.
—— *revilli*, 186.
Pyrrhulopsis, 226, 227, 232, 245, 249, 250, 255, 258, 262, 263.
Pyrrhulopsis personata, 225, 230, 234, 242, 266.
—— *splendens*, 224, 225, 230, 234, 242, 266.
Pyrrhura, 224, 226, 227, 239, 245, 249, 252, 253, 254, 262, 263, 266.
—— *leucotis*, 224, 228, 234, 239, 274, 278.
Rana, 50.
Ranodon, 42.
Rhachianectes, 106.
Rhea, 261.
Rhynchocephalus, 73.
Rhynchops, 2.
Rhynchosaurus, 4.
Rhynchotus, 261.
Rhytidoceros, 261.
Samotherium, 288, 289, 293, 296, 303, 305.
Saphæosaurus, 54.
Sarcodaces odoë, Nesting-habits of, 115, 130, 132, 136.
Sarsiella ornithoides, 189, 206.
Sauranodon, 3, 54.
Sauromalus, 23.
Schilbe mystus, 137.
Sclerocephalus, 69, 71.
Simochromis diagramma, 141, 156.
Sivatherium, 288, 289, 292, 293, 296.
Spathodus erythrodon, 141.
Spheniscus, 261.
Sphenodon diversum, 72.
—— *güntheri*, 72, 73.
—— *punctatus*, on the Development of the Skeleton of; with Remarks on the Egg, on the Hatching, and on the Hatched Young, 1–86.
—— (*Hatteria*) *punctatus*, 74.
Stellio, 30.
Stereosternum, 36.
Stringops, 217, 218, 225, 226, 227, 230, 236, 243, 245, 248, 253, 254, 255, 256, 258, 259, 261, 262, 263, 268.
—— *habroptilus*, 216, 228, 233, 272, 274, 276.
Strix, 365.
Struthio, 261.
Sus, 289.
Swinnerton, H. H., and Howes, G. B. On the Development of the Skeleton of the Tuatara, *Sphenodon punctatus*; with Remarks on the Egg, on the Hatching, and on the Hatched Young, 1–86.

Sylvania mitrata, 360.
Synodontis granulosus, 140, 149, 170.
—— *multipunctatus*, 140, 149.
—— *ornatipinnis*, 137.
—— *zambesensis*, 137.
Syrnium, 361, 362.
Tanganyika (Lake), Third Contribution to the Ichthyology of.—Report on the Collection of Fishes made by Mr. J. E. S. Moore in, 137–178.
Tanygnathus, 226, 227, 234, 245, 249, 253, 255, 259, 261, 262, 263, 266.
—— *mülleri*, 222, 231, 240.
Telmatochromis temporalis, 141, 156.
—— *vittatus*, 141.
Tetraceros, 292.
Thamnophilus, 396.
Tilapia boops, 141, 158, 176.
—— *burtoni*, 138, 141, 157.
—— *dardennii*, 141, 157.
—— *grandoculis*, 141.
—— *horii*, 141.
—— *labiata*, 141, 157.
—— *microlepis*, 141, 158.
—— *natalensis*, 137.
—— *nilotica*, 138, 141, 157.
—— *pleurotænia*, 141, 157, 174.
Tilapia polyacanthus, 137.
—— *rubropunctata*, 141.
—— *trematocephala*, 141, 157, 176.
Tongue, Mudge on the Myology of the Parrots', 211–278.
Trematocara marginatum, 141, 155.
—— *unimaculatum*, 141, 155, 174.
Triton, 50.
Tropheus annectens, 141.
—— *moorii*, 141.
Tuatara, on the Development of the Skeleton of the; with Remarks on the Egg, on the Hatching, and on the Hatched Young, 1–86.
Tupinambis, 15, 57.
Tylosaurus, 14.
—— *dyspelor*, 34.
Vanga, 396.
Varanus, 57.
Vini, 226, 227, 243, 249, 254, 255, 257, 259, 261, 262, 263.
—— *australis*, 225, 232, 234, 242, 245, 266.
Whale (Pigmy), Osteology of the, 87–114.
Xenochromis hecqui, 141, 159.
Xenotilapia ornatipinnis, 141, 154, 174.
—— *sima*, 141, 155.
Zootoca, 41, 53, 56.

END OF VOLUME XVI.

PRINTED BY TAYLOR AND FRANCIS, RED LION COURT, FLEET STREET.

TRANSACTIONS OF THE ZOOLOGICAL SOCIETY OF LONDON

(continued).

	To Fellows. £ s. d.	To the Public. £ s. d.
VOLUME XIV. (1896–1898, containing 47 Plates) . Price	5 5 0	7 0 0
Part 1. (1896, containing 2 Plates) . . . . . „	0 6 0	0 8 0
„ 2. (1896, containing 6 Plates) . . . . . „	0 9 0	0 12 0
„ 3. (1897, containing 9 Plates) . . . . . „	0 15 9	1 1 0
„ 4. (1897, containing 10 Plates) . . . . . „	1 10 0	2 0 0
„ 5. (1898, containing 2 Plates) . . . . . „	0 6 0	0 8 0
„ 6. (1898, containing 7 Plates) . . . . . „	0 18 0	1 4 0
„ 7. (1898, containing 6 Plates) . . . . . „	0 11 3	0 15 0
„ 8. (1898, containing 5 Plates and Title and Index) „	0 9 0	0 12 0
VOLUME XV. (1898–1901, containing 52 Plates) . Price	5 15 6	7 14 0
Part 1. (1898, containing 8 Plates) . . . . . „	0 15 9	1 1 0
„ 2. (1899, containing 5 Plates) . . . . . „	0 9 0	0 12 0
„ 3. (1899, containing 4 Plates) . . . . . „	0 9 0	0 12 0
„ 4. (1899, containing 4 Plates) . . . . . „	0 9 0	0 12 0
„ 5. (1900, containing 24 Plates) . . . . . „	2 12 6	3 10 0
„ 6. (1901, containing 4 Plates) . . . . . „	0 11 3	0 15 0
„ 7. (1901, containing 3 Plates and Title and Index) „	0 9 0	0 12 0
VOLUME XVI. (1901–1903, containing 38 Plates) . Price	5 8 0	7 4 0
Part 1. (1901, containing 6 Plates) . . . . . „	0 18 0	1 4 0
„ 2. (1901, containing 5 Plates) . . . . . „	0 11 3	0 15 0
„ 3. (1901, containing 9 Plates) . . . . . „	0 15 9	1 1 0
„ 4. (1902, containing 5 Plates) . . . . . „	0 9 0	0 12 0
„ 5. (1902, containing 4 Plates) . . . . . „	0 13 6	0 18 0
„ 6. (1902, containing 3 Plates) . . . . . „	0 15 9	1 1 0
„ 7. (1902, containing 3 Plates) . . . . . „	0 11 3	0 15 0
„ 8. (1903, containing 3 Plates and Title and Index) „	0 13 6	0 18 0

CONTENTS.

IX. *Ecdysis, as Morphological Evidence of the Original Tetradactyle Feathering of the Bird's Fore-limb, based especially on the Perennial Moult in* Gymnorhina tibicen. *By* EDWARD DEGEN, *F.Z.S.* (Plates XXXVI.–XXXVIII.) page 347

List of the Papers contained in Vol. XVI. 419

Index of Species, &c. in Vol. XVI. 421

Titlepage and Contents to Vol. XVI.

THE PUBLICATIONS OF THE ZOOLOGICAL SOCIETY OF LONDON.

The scientific publications of the Zoological Society of London are of two kinds—"Proceedings," published in an octavo form, and "Transactions," in quarto.

According to the present arrangements, the "Proceedings" contain not only notices of all business transacted at the scientific meetings, but also all the papers read at such meetings and recommended to be published in the "Proceedings" by the Committee of Publication. A large number of coloured plates and engravings are attached to each annual volume of the "Proceedings," to illustrate the new or otherwise remarkable species of animals described in them. Among such illustrations, figures of the new or rare species acquired in a living state for the Society's Gardens are often given.

The "Proceedings" for each year are issued in four parts, on the first of the months of June, August, October, and April, the part published in April completing the volume for the last half of the preceding year. Commencing from January 1901 they form two half-yearly volumes.

The "Transactions" contain such of the more important communications made to the scientific meetings of the Society as, on account of the nature of the plates required to illustrate them, are better adapted for publication in the quarto form. They are issued at irregular intervals.

Fellows and Corresponding Members, upon payment of a Subscription of £1 1*s.* before the day of the Anniversary Meeting in each year, are entitled to receive all the Society's Publications for the year. They are likewise entitled to purchase the Publications of the Society at 25 per cent. less than the price charged for them to the Public. A further reduction of 25 per cent. is made upon purchases of Publications issued prior to 1871, if they exceed the value of five pounds.

Fellows also have the privilege of subscribing to the Annual Volume of the 'Zoological Record' for a sum of £1 (which includes delivery in the United Kingdom *only*), but this privilege only holds good if the subscription is paid before the First of December in each year.

Such of these publications as are in stock may be obtained at the Society's Office (3 Hanover Square, W.), at Messrs. Longmans', the Society's publishers (Paternoster Row, E.C.), or through any bookseller.

May, 1903.

P. CHALMERS MITCHELL,
Secretary.

918

SMITHSONIAN INSTITUTION LIBRARIES
3 9088 00850 0043